

RELATIONSHIPS OF THE STOMIIFORM FISHES (TELEOSTEI), WITH A DESCRIPTION OF *DIPLOPHOS*

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ABSTRACT. A primarily osteological description is provided for two species of the phylogenetically and morphologically primitive stomiiform teleost genus *Diplophos*. Evidence is presented to document the monophyly of two major teleostean groups, the Stomiiformes and the Neoteleostei. Monophyly of the Eurypterygii (*sensu* Rosen, 1973) is evaluated and tentatively accepted. Stomiiforms, previously placed by most authors as a suborder (Stomiatoidei) of the Protacanthopterygii, are found to be neoteleosts; they comprise the sister group of all other neoteleosts, the Eurypterygii. The Protacanthopterygii (comprising the Esocoidei, Argentinoidei, and Salmonoidei, including the Salmonoidea and Osmeroidea, *sensu* Rosen, 1974) is not supported as monophyletic. Alternative hypotheses of "protacanthopterygian" relationships are suggested and discussed.

INTRODUCTION

The group of teleosts herein termed Stomiiformes comprises a significant portion of the oceanic vertebrate fauna. The group consists of mesopelagic and bathypelagic fishes and currently includes 9 families, 50 genera, and over 300 species. Stomiiforms are found in all of the major ocean basins; adults range in size from about 15 mm to nearly 500 mm in length. The group has been the subject of extensive research, including distributional studies and systematics at all taxonomic levels (e.g., Baird, 1971; Baird and Eckardt, 1972; Gibbs, 1969; Goodyear and Gibbs, 1970; Morrow and Gibbs, 1964; Mukhacheva, 1978; Parin *et al.*, 1977; Parin and Pokhilskaya, 1974, 1978; Weitzman, 1967a, b, 1974), studies in photobiology and vision (e.g., Baguet and

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Marechal, 1976; Fernandez, 1978; Hansen, 1970; Jørgensen and Munk, 1979; Lockett, 1977; O'Day, 1973), in ecology (e.g., Clarke, 1974, 1978; DeWitt and Cailliet, 1972; Hopkins and Baird, 1973; Merrett and Roe, 1974), in biochemistry and physiology (e.g., Blaxter *et al.*, 1971; Childress and Nygaard, 1973; Douglas *et al.*, 1976), and in fisheries (e.g., Gjøsaeter and Kawaguchi, 1980). The degree of morphological diversity and extent of specialization in body form and feeding structures makes the group an excellent model for studies concerned with evolution in general, but especially evolution in the oceanic environment.

It is becoming widely accepted that phylogenetic analyses of relationship are crucial to and must precede explication of evolutionary patterns and subsequent discussions of evolutionary mechanisms (e.g., Eldredge and Cracraft, 1980; Lauder, 1981; Wiley, 1981). Only recently have explicitly phylogenetic methods been used to elucidate relationships within the Stomiiformes (Weitzman, 1974; Fink, 1976, and in preparation). The phylogenetic relationship of the Stomiiformes to other teleosts has been examined by Rosen (1973). In order to facilitate future phylogenetic and evolutionary studies on the group, we reconsider stomiiform relationships *vis à vis* other teleosts and provide a diagnosis of the group using phylogenetic methodology.

The nomenclature used herein reflects the findings of Steyskal (1980) regarding formation of suprageneric names based on the name *Stomias*. Steyskal (p. 172) found that the traditional usage, such as Stomiidae or Stomiiformes (Rosen, 1973), is incorrect and these names should be amended to Stomiidae and Stomiiformes, following the International Code of Zoological Nomenclature.

There are three major sections to this paper. First, there is an osteological description of specimens of *Diplophos*, which we consider representative of phy-

logenetically and morphologically primitive stomiiforms (see Fig. 1). Second, we present evidence bearing on the monophyly of the Stomiiformes and on the relationships of the group with other teleosts. Finally, we evaluate recent hypotheses of relationships within the Protacanthopterygii based on the evidence we have encountered during our investigation of stomiiform relationships.

Our recognition of *Diplophos* species as representative of morphologically and phylogenetically primitive stomiiforms is based on outgroup comparisons. We surveyed the morphology of members of the Stomiiformes and of numerous primitive teleosts in order to determine the distributions of traits among them. The stomiiform genus whose members share the fewest characters with other stomiiforms and thus the most characters with other primitive teleosts is *Diplophos*. It is possible that *Diplophos* is not monophyletic, since no derived characters have ever been used in its diagnosis. Should the genus be monophyletic, the character distribution we find suggests that *Diplophos* is the sister group of all other stomiiforms; however, a documented statement of that hypothesis and a diagnosis of the genus is not included herein, pending further work on the genera included by Weitzman (1974) in the Gonostomatidae and Photichthyidae. Our study does not include a critical examination of those families (which were not diagnosed by Weitzman), and *Diplophos* may eventually be found to be a member of some primitive stomiiform subgroup. However, the usefulness of *Diplophos* species as representative of relatively primitive stomiiforms is not dependent upon precise hypotheses of their phylogenetic relationships. The four known species of *Diplophos* have been examined by us and were reviewed by Mukhacheva (1978).

Our concept of relationships is phylogenetic (*sensu* Hennig, 1966). Use of the word primitive in the text, unless other-

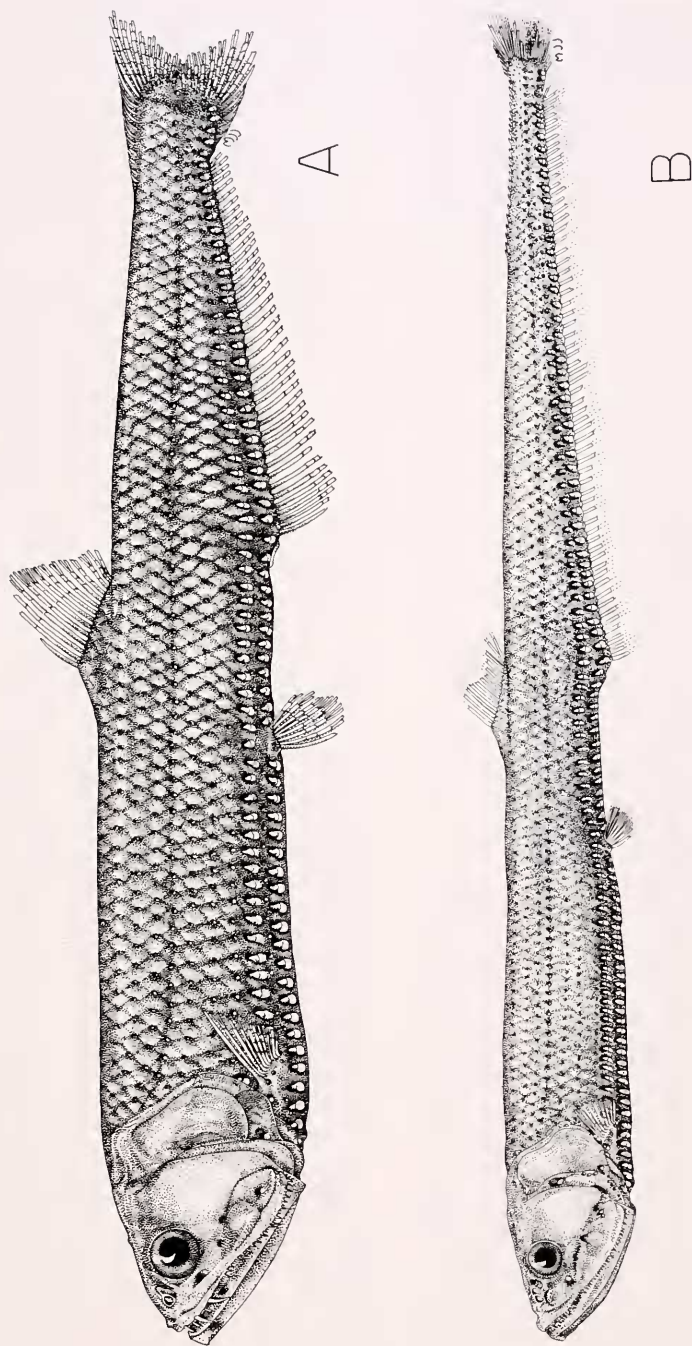


Figure 1. A. *Diplophos maderensis* (USNM 186364; 114.0 mm SL). B. *Diplophos taenia* (USNM 203292; 83.4 mm SL).

wise qualified, refers to phylogenetically primitive. Characters used to diagnose groups (synapomorphies) were chosen by comparison with numerous species in appropriate outgroups. Specimens examined are listed in the Appendix.

In later sections we present arguments for use as synapomorphies certain similarities among the various teleosts discussed. We have concentrated our search for characters and the discussion below on what we believe to be primitive members of their lineages, based on outgroup comparisons. We surveyed more derived members of each group, as well, to try to ensure that the characters we were using as synapomorphies for each lineage were not instead synapomorphies for some relatively primitive subgroup within that lineage. Also, we have tried to point to instances of "convergence," when characters used as synapomorphies for a group also appear to be present in other lineages. Recognition of convergence is based on parsimony criteria, and our justification is presented for each case.

We have not utilized evolutionary "trends" or "tendencies" as characters. Usually implicit in these concepts is the assumption that primitive members of the group lack a character while more derived members have it. In such a case, however, presence of the character would actually diagnose some subgroup(s) within a larger group. When a character "trend" is based on a character which is present but less elaborated in primitive members, we would use presence of the character in its primitive form to diagnose the group and presence of the more elaborated character to diagnose a subgroup.

Rosen's conclusion (1973), with which we agree, that stomiiforms represent a lineage separate from the Protacanthopterygii, in which the "Stomiatoidei" has generally been placed, required a change to ordinal rank for the group. This would seem to necessitate comparable changes in rank for many of the groups recognized

by Weitzman (1974), but we prefer to retain his ranking of taxa at the infraordinal level and below, pending work on relationships of the genera of primitive stomiiforms and publication of the senior author's work on the "Stomiatoidea."

In the description of *Diplophos*, bones are listed as paired or unpaired; descriptions of paired bones are for one member of the pair.

Most of the specimens used in this study were cleared and stained, using a modified version of the enzyme technique of Taylor (1967). The illustrations were prepared with the use of camera lucida with Wild M-5 or Zeiss IV-B Zoom microscopes; a Leitz Widefield stereomicroscope was used for detailed observations.

DESCRIPTION OF *DIPLOPHOS*

ETHMOID REGION

The ethmoid cartilage forms the core of the anterior region of the neurocranium (Figs. 2-4). In dorsal view, the ethmoid cartilage has three major features: an anterior, broad lateral concavity, the lateral prenasal process, and a deeply concave recess for the nasal capsule. In dorsal view the profile of the anterior border of the ethmoid cartilage lies at about a 90° angle to the longitudinal body axis, paralleling the anterior border of the vomer. At the midline, the ethmoid cartilage is dorsoventrally shallowest anteriorly, gaining in thickness posteriorly, and reaching its greatest thickness just posterior to the level of the lateral prenasal processes. There are two major lateral extensions of the ethmoid cartilage: the lateral prenasal processes and the lamina orbitonasalis. Anterior to the prenasal processes, the anterodorsal ethmoid surface is broadly concave, forming an articular surface for the maxilla. Between the prenasal process and the lamina orbitonasalis is the deeply concave olfactory recess. Within the posterior wall of the olfactory recess is the foramen

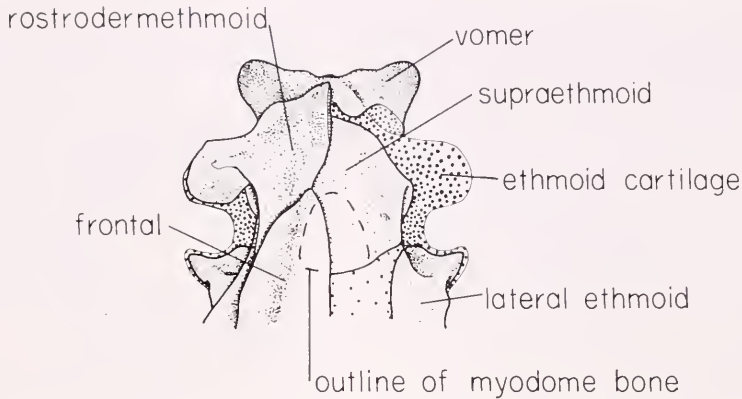


Figure 2. Ethmoid region of *D. taenia* (USNM 206614; 171.0 mm SL), dorsal view; right portion of rostrodermethmoid removed.

olfactorium advehens, through which the olfactory nerve passes. The posterior surface of the ethmoid cartilage has a single, medial deep conical recess, the anterior myodome, in which the superior oblique eye muscles have their point of origin. Posterior to the lamina orbitonasalis, the cartilage is continuous with the trabeculum communis (Fig. 5) ventrally and the orbital cartilages dorsally. The trabeculum communis extends posteriorly from the ethmoid cartilage and lies just dorsal to the parasphenoid bone. A membranous interorbital septum extends from the trabeculum communis to the frontal bones above the orbit.

The ethmoid ossifications include a single supraethmoid, a single rostrodermethmoid, a single ventral ethmoid, paired lateral ethmoids, and a single anterior myodome bone. The supraethmoid is a perichondral ossification on the dorsal cartilage surface. Posteriorly, the supraethmoid has a slightly convex border, and its lateral edges meet the postero-medial borders of the olfactory recesses. Anteriorly, the supraethmoid border is more convex than the posterior border, and its lateral edges meet the anteromedial border of the olfactory recesses. The supraethmoid ossification also covers the medial surface of the olfactory recess as

the capsular portion of the supraethmoid. This capsular portion, primarily endochondral, is an approximately cone-shaped object with its apex near the dorsal midline. Laterally, the capsular portion is highly fenestrated. (In some more specialized stomiiforms and in the osmerid *Spirinchus*, the capsular portion of the supraethmoid is separate from the dorsal portion; Weitzman, 1967: 509, Fig. 1.)

The dermal rostrodermethmoid is a bone formed by fusion of the paired dermethmoids with the single rostral (Patterson, 1975: 511). The anteromedial "rostral" section extends anterior to and between the "dermethmoid" portions. Thus, there is a medial ramus between the dermethmoid portions which extends a distance about equal to one-quarter of their length in an anteroposterior axis. Each lateral portion of the ossification is essentially composed of two large rami, both of which partially overlie the supraethmoid. The lateral ramus is fenestrated, with its anterior border overlying the anterior border of the ethmoid cartilage and its posterior border overlying the anterior border of the olfactory recess; its lateral apex reaches near the lateralmost border of the prenasal process of the ethmoid cartilage. The posterior

rostrodermethmoid ramus is smooth and extends posteriorly to overlap the frontal. The lateral border of the posterior ramus overlies the medial border of the olfactory recess; the medial border is slightly convex and extends towards the midline to the point where the posterior rami of the rostrodermethmoids meet. The posterior ramus reaches to a point just dorsal to the vertical ramus of the lateral ethmoid. Anteriorly, the rostral portion reaches very near to the vomer.

Weitzman (1967a) considered the presence of two, separate "proethmoids" (= lateral dermethmoids of Patterson, 1975) to be primitive within the Protacanthopterygii. However, Patterson (1975: 511–512) found that fusion of the rostral and lateral dermethmoids into a single bone (the rostrodermethmoid) is primitive within teleosts. In most teleosts the ethmoid commissure is absent, but in *Megalops*, at least, it is present (see Patterson, 1975, Fig. 140). We agree with Patterson that the presence of two separated "proethmoids" of some osmeroids and stomiiforms is a derived feature. We further suggest that "proethmoids" result from reduction or loss of the rostral portion of the rostrodermethmoid. This loss has occurred independently in osmeroids and stomiiforms, since in *Diplophos* and some other primitive stomiiforms such as *Gonostoma*, *Photichthys*, and *Triplophos*, and in some osmeroids such as *Hypomesus*, there is a single rostrodermethmoid. In *Osmerus* (MCZ 56535) we find the two "proethmoids" as described by Weitzman (1967a: 509), but in addition find a small but well-developed triangular ossification lying anteromedial to the "proethmoids"; we take this small bone to be the rostral element. In a post-larval specimen of *Diplophos taenia* (34 mm SL; MCZ 52548), we see what appears to be a small, chevron-shaped ossification lying adjacent and anteromedial to the lateral dermethmoids; we are unable to clearly discern joint lines completely around this ossification, but propose that

it is the rostral element which is partially (or completely?) joined to the lateral dermethmoids.

The conclusion that we have reached regarding the phylogenetic history of the lateral and rostral dermal ethmoid ossifications leads us to call the lateral ossifications lateral dermethmoids rather than proethmoids (as done by Weitzman, 1967a). This more clearly indicates their homology with the lateral dermethmoids of primitive teleosts.

Also, *contra* Weitzman's (1967a: 519) statement that the "lateral supraethmoid process" (=rostrodermethmoid, herein) is fused to the supraethmoid in large specimens of *Polymetme*, we find the rostrodermethmoid autogenous in specimens of *Polymetme* that we have examined, but note that the bones are indeed tightly joined in adults.

The ventral ethmoid is a single, median perichondral ossification that lies dorsal to and fuses with the vomer during ontogeny. The anterior border of the ventral ethmoid lies ventral to the anterior border of the ethmoid cartilage; in that area, in adults, the ossification is fused to the vomer. There are bilateral, posterolaterally projecting broad rami, almost triangular from ventral aspect, which extend over most of the dorsal surface of the vomer, and beyond the border of the vomer, posterolaterally.

The anterior myodome bone lines the conical myodome cavity in the posterior wall of the ethmoid cartilage. The ossification extends anteriorly to a point near the anteromedial apices of the capsular portions of the supraethmoid. The posterior border expands to near the level of the posteroventral border of the capsular portion of the supraethmoid, and ventrally to the level of the posterior border of the supraethmoid.

The lateral ethmoids are paired, perichondral ossifications. The following description is of one side only, but applies equally to the other. The bone covers the anterior and posterior surfaces of the lam-

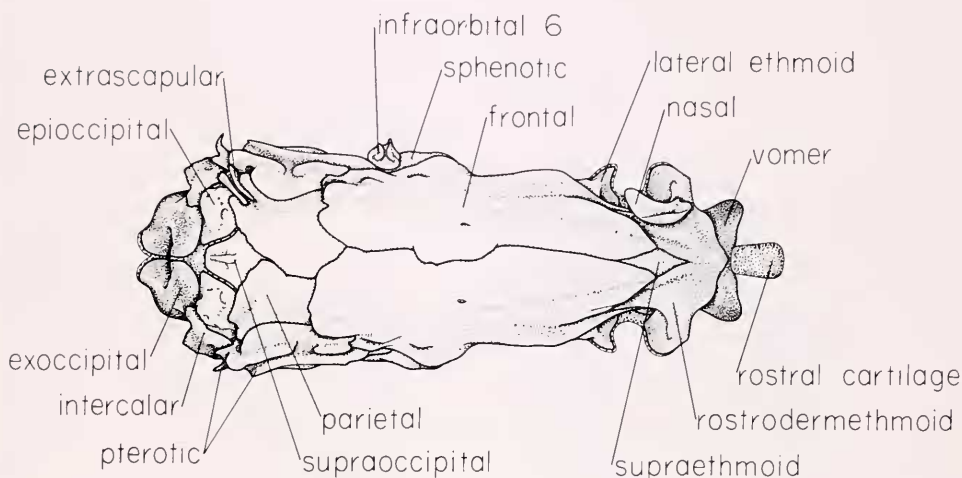


Figure 3. Neurocranium of *D. taenia* (USNM 206614; 171.0 mm SL), dorsal view. Infraorbital 6 = dermosphenotic of authors.

ina orbitonasalis, thus lining the posterior wall of the nasal capsule and the anterior wall of the orbit. Within the nasal recess, the lateral ethmoid ossification extends to the lateral border of the foramen olfactorium advehens and is continuous through the lateral wall of the foramen with the ossification on the posterior wall of the lamina orbitonasalis. Anterodorsally the lateral ethmoid extends to a point about one-third of the way around the concave dorsoposterior border of the olfactory recess. Posteriorly, the lateral ethmoid ossification extends about one-fourth the length of the dorsal wall of the orbital cavity.

The vomer (Figs. 2–4, 13) is a median bone which lies ventral to the ethmoid cartilage. It is a compound bone composed of the ventral ethmoid and vomer proper (see ventral ethmoid, above). Anteriorly the vomer is relatively wide, with two broad lateral rami which anteriorly lie ventral to the anterior border of the ethmoid cartilage. Each ramus has one to three conical teeth ankylosed to it laterally (Fig. 4). Anteromedially the vomer extends dorsally over the anterior border of the ethmoid cartilage to nearly reach the rostrodermethmoid, to which it is

tightly bound by thick connective tissue. Posteriorly, the vomer tapers to an elongate, sharply-pointed median ramus that extends to about the level of the anterior wall of the orbit and is enclosed dorsally by the parasphenoid. A thick median fibrocartilage body, the rostral cartilage, lies between the anterodorsal surface of the ethmoid region and the posterior surfaces of the premaxillary bones.

FRONTAL AND PARIETAL

The frontal bones are paired dermal ossifications that form the major portion of the skull roof (Figs. 3, 4, 6). Anteriorly the frontal extends partially over the ethmoid cartilage, reaching a point about equal to the anterior extension of the anterior myodome bone. Anterolaterally the frontal lies dorsal to the medial border of the nasal recess and dorsal to the lateral ethmoid. More posteriorly, the frontal overlies the tectum cranii and forms the lateral border of the skull roof and the dorsal border of the orbit. At the posterodorsal border of the orbit, the frontal curves medially, with its posterior border ranging in various individuals from deeply convex to relatively straight,

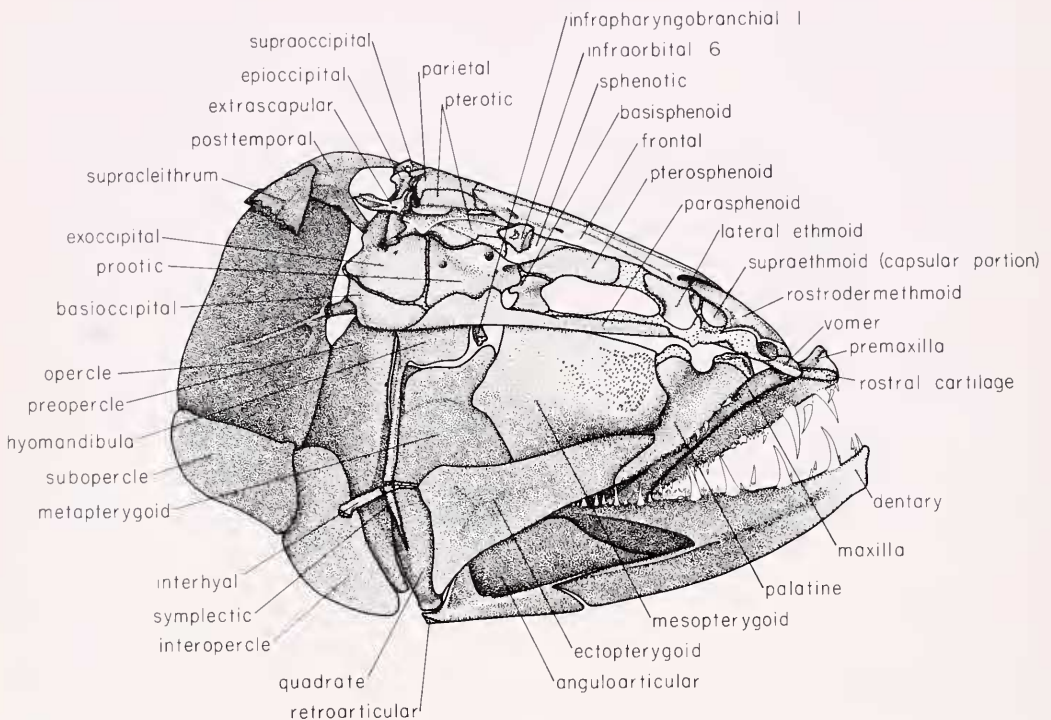


Figure 4. Neurocranium (lateral view) and suspensorium (medial view) of *D. taenia* (USNM 206614; 171.0 mm SL). Infraorbital 6 = dermosphenotic of authors.

at about a 90° angle to the longitudinal body axis. The posterior frontal border lies at a point about one-fifth the length of the neurocranium from its posterior border. Medially, the frontals meet in an irregular articulation and partially overlap one another. The frontals partially overlie the following bones: supraethmoid, lateral ethmoids, sphenotics, pterotics, and parietals.

The supraorbital sensory canal lies on the dorsal surface of the frontal and is enclosed in bone for about one-third its length in small specimens and is nearly enclosed for much of the length of the frontal in large specimens.

The parietals are paired dermal ossifications forming the dorsal surface of about the posterior quadrant of the neurocranium (Figs. 3–7). The parietal is roughly square in dorsal view. The anterior border lies ventral to the frontal, is

irregular, and lies at approximately a 90° angle to the longitudinal body axis. The lateral border is superficially overlain by the pterotic and lies more or less parallel to the longitudinal body axis. Just lateral to the mid-length of the parietal, there is a deep concave facet in which the pterotic articulates. There is a deep notch in the posterolateral border for passage of a sensory canal. The posterior parietal border articulates with the epioccipital posterolaterally and with the supraoccipital posteromedially. The parietals broadly overlap at the dorsal midline.

PTEROSPHEOID, SPHENOTIC, PARASPHEOID, BASISPHEOID, AND POSTERIOR MYODOME

The pterosphenoids are paired ossifications that form the posterodorsal wall of the orbits (Figs. 4–6). There is an an-

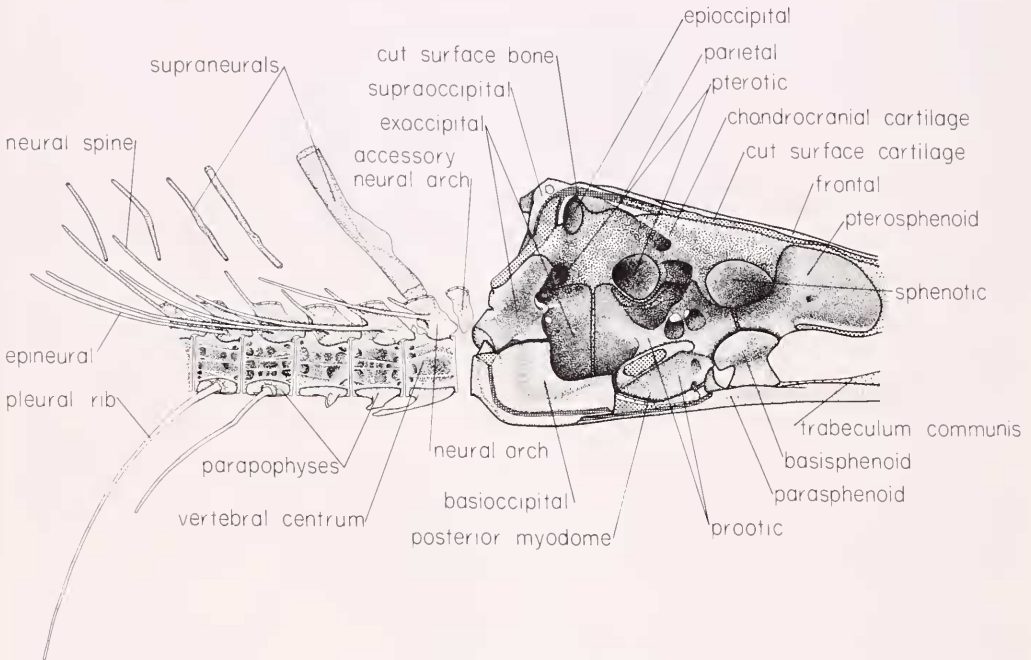


Figure 5. Neurocranium (internal view) and anterior vertebrae (lateral view) of *D. taenia* (USNM 206614; 171.0 mm SL).

terior perichondral portion that encloses much of the orbital cartilage. The pterosphenoid reaches a level just anterior to the midpoint of the orbit. Anteroventrally there is a synchondral joint with the contralateral pterosphenoid; posteroventrally there is a synchondral joint with the basisphenoid. The dorsal perichondral border is very broadly convex; posteriorly it articulates synchondrally with the prootic; posterodorsally it articulates synchondrally with the sphenotic; dorsally it approaches or articulates with the frontal. Anterodorsal to its articulation with the basisphenoid, the pterosphenoid has a deep concavity which forms the dorsal border of the optic foramen.

In medial aspect the pterosphenoid forms the floor and ventrolateral walls of the cranial fossa (Figs. 5, 6). The dorsal surface of the bone is shallowly concave anteriorly and posteriorly; between these concavities the bone has a small dorsal rise that extends dorsolaterally.

The sphenotics are paired bones, posterolaterally articulating synchondrally with the pterosphenoids and anterolaterally articulating synchondrally with the prootics; they form the posterolateral border to the orbital fossa (Figs. 3–6). Anteriorly the sphenotic lies more or less horizontally, with vertical perichondral ossifications lining the posterodorsal roof of the orbital fossa and dorsal ossifications forming the lateral border of the neurocranium (the sphenotic is almost completely overlain by the frontal). The posterior half of the sphenotic extends more ventrally and medially than the anterior half; it extends ventrally to join the prootic synchondrally and (endochondrally) extends medially to form part of the lateral wall of the cranial fossa (Fig. 5). The posteroventral border of the sphenotic is slightly to deeply concave; medial to this concavity is the articulation of the hyomandibula (the hyomandibular fossa). In medial aspect, the

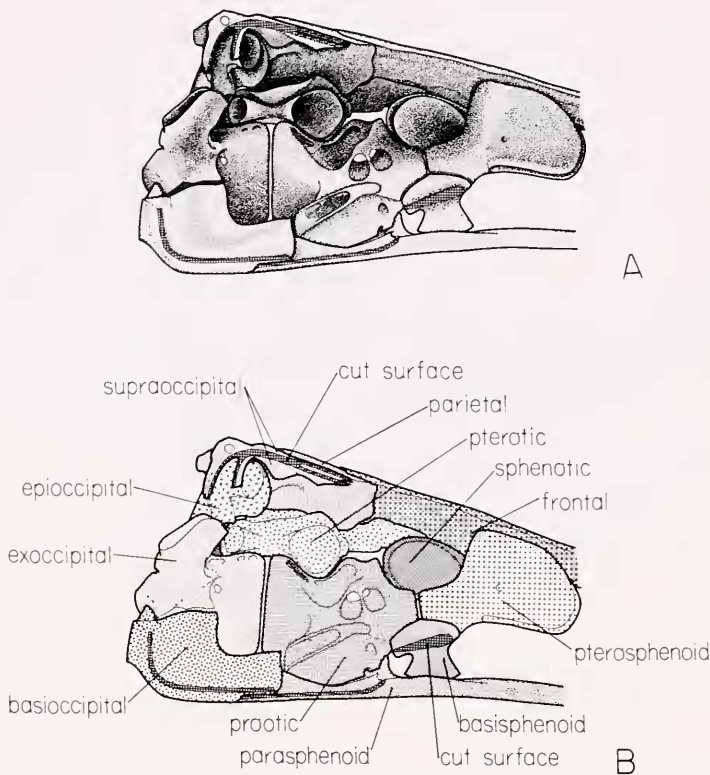


Figure 6. A. Neurocranium of *D. taenia* (USNM 206614; 171.0 mm SL), internal view; cartilage not shown. B. Same as A, with each bone represented by a symbol pattern.

sphenotic is deeply concave; posteriorly, there is a small conical fossa against which lies the anterior portion of the anterior vertical semicircular canal. In *D. maderensis*, *D. greyae*, and *D. rebaini*, the cartilaginous chondrocranium lies between the sphenotic and the brain cavity; in *D. taenia*, no cartilage is present in that area and bone is visible on the medial surface of the braincase (Fig. 5).

The parasphenoid is a single, relatively straight median bone (Fig. 4). Anteriorly, the parasphenoid lies just ventral to the ethmoid cartilage, approaching its anterior border. More posteriorly the parasphenoid extends ventral to the trabeculum communis to form the medial floor of the orbit. The ventral surface of the parasphenoid is concave in the region ventral to the posterior areas of the eth-

moid cartilage and orbit; the vomer articulates in this concavity. At a point about the mid-length of the orbit (in *D. maderensis*) or posterior to that point (in *D. taenia*) there is a bilateral flange of bone that enlarges posteriorly; each flange extends up to meet and lie lateral to the basisphenoid and then continues as a lateral wing that lies lateral to and is tightly articulated with the prootic and basioccipital. The posterior extension of the parasphenoid lies medial to about the midpoint of the otic bullae.

The basisphenoid consists of a single ventral ramus and broad, short bilateral dorsal rami (Figs. 4–6). The ventral ramus extends over the trabeculum communis and enters the orbital cavity; the ventral border of the basisphenoid ossification is either slightly convex or more

or less straight and horizontal, curving dorsally anteriorly, and reaching to about the level of the dorsal border of the lateral parasphenoid wing. The dorsal rami extend laterally, anterodorsally articulating synchondrally with the pterosphenoids posterodorsally and posteriorly lying medial to and articulating diarthrally with the prootic. From lateral aspect the anterior basisphenoid border is concave, the posterior border more deeply so; the dorsal border is broadly convex (see Figs. 5, 6). The anteromedian border of each lateral ramus is deeply concave and forms the ventral border of the optic foramen. Between the posterior border of the ventral basisphenoid ramus and the prootic and parasphenoid, there is a hiatus; in more derived stomiiforms this hiatus is relatively large and is termed the post-basisphenoid space of Weitzman (1967a).

The medial surface of the basisphenoid, facing the cranial fossa, is deeply concave.

The posterior myodome is relatively large and deep (Figs. 5, 6). Anteriorly the myodome extends dorsally as far as the dorsoventral surfaces of the lateral basisphenoid rami. Posteriorly, the dorsal roof of the myodome is formed by the medial prootic laminae. The floor of the myodome is formed by the parasphenoid and its lateral extensions. The lateral wall of the myodome is formed by the prootic and parasphenoid; the medial wall is formed by the prootic. The posterior termination of the myodome lies at about the midpoint between the anterior border of the lateral parasphenoid wing and the posterior border of the parasphenoid.

OTIC AND OCCIPITAL REGIONS AND POSTTEMPORAL FOSSA

The supraoccipital is a single median bone lying at the dorsoposterior apex of the skull (Figs. 3–7). From posterior view, the bone is roughly triangular, with a ventral apex; it has synchondral artic-

ulations with the epioccipitals along its posterolateral borders. Dorsally, the supraoccipital is very broadly convex, with about half of its area overlain by the parietals. There is a very small supraoccipital crest.

The medial surface of the supraoccipital forms the internal posterodorsal roof of the cranial fossa. There is a perichondrally lightly ossified area which curves around the dorsal portion of the posterior vertical semicircular canal.

The epioccipitals (=epiotics, *sensu lato*; see Patterson, 1975: 425) are paired, perichondral ossifications that form the dorsoposterior part of the braincase and contain the posterior vertical semicircular canals (Figs. 3, 4, 6, 7). The epioccipital has synchondral joints with the supraoccipital medially, the pterotic laterally, and the exoccipital ventrally. The posteroventral surface of the intercalar articulates syndesmotically with the epioccipital.

The medial surface of the epioccipital consists primarily of a perichondrally ossified canal through which passes the posterior vertical semicircular canal (Fig. 5).

The exoccipitals are paired bones which form the largest portion of the posterior of the skull (Figs. 3–7). There are synchondral joints with the epioccipitals dorsally, the pterotic anterodorsally, the contralateral exoccipital medially, the prootic anterolaterally, and the basioccipital ventrally. The intercalar overlies the posterodorsal and dorsolateral exoccipital surfaces and articulates in a thick syndesmotic joint. The anterior border of the exoccipital, adjacent to the prootic, is nearly vertical to the longitudinal body axis; the ventral border, adjacent to the basioccipital, is nearly horizontal. The dorsal border extends laterally and ventrally at the posterolateral corner of the neurocranium, then is broadly convex along the posterior region of the skull. The posteromedial border is vertical dorsally, then deeply concave where it forms

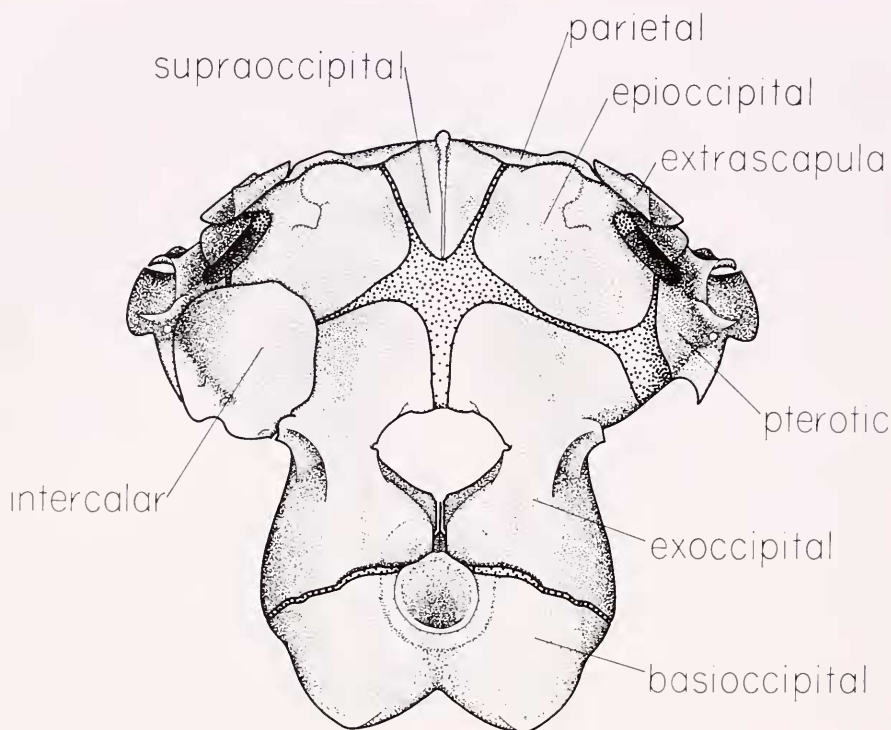


Figure 7. Neurocranium of *D. taenia* (USNM 206614; 171.0 mm SL), posterior view.

the border of the foramen magnum, excluding the basioccipital from the foramen magnum. Ventral to the foramen magnum, the exoccipital bears a wide articular facet which forms, with the basioccipital (see below), a deeply concave articular surface for the notochord. The foramen for the ninth and tenth cranial nerves is a prominent feature of the exoccipital (Fig. 7).

The medial surface of the exoccipital forms the posterolateral and posterodorsal walls of a deep cavity which contains the saccular and lagenar portions of the ear. In addition, there is a deep concavity dorsolaterally on the exoccipital in which lies the ampulla at the junction of the posterior portions of the horizontal and posterior vertical semicircular canals.

The basioccipital is a single bone which forms the posterior floor of the neurocranium (Figs. 4–7). Anteriorly, the

basioccipital extends to a point about midway between the posterior surface of the neurocranium and the anteroventral border of the prootic. Anteroventrally the basioccipital lies dorsal to the parasphenoid, which is tightly joined to it syndesmotically and synchondrally. The broadly concave anterior border of the basioccipital has a synchondral joint with the prootic; the nearly straight dorsal border has a synchondral joint with the exoccipital. Posteriorly the basioccipital has a deeply concave articular surface for the notochord. The basioccipital forms the floor of the lagenar capsule.

The shape of the basioccipital in medial view is illustrated in Figures 5 and 6. There are bilateral, very deep concavities in the bone in which lie the saccular and lagenar portions of the ear. The large medial flange of bone separating the two concavities is visible in Figure 7 just ven-

tral to the foramen magnum and medial to the posteromedial borders of the exoccipitals.

The intercalars are paired dermal bones which overlay and have tight syndesmotic joints with the epioccipitals, pterotics, and exoccipitals (Figs. 3, 7). The posterolateral apex of the intercalar is a process which serves as the attachment site for the ligament extending from the anteroventral ramus of the posttemporal.

The prootics are paired bones which form much of the lateral walls of the braincase (Figs. 4–6). Ventrally, the prootic lies medial to, and has a broad syndesmotic articulation with, the parasphenoid. The prootic has synchondral articulations with the basisphenoid anteroventrally, the pterosphenoid anterodorsally, the sphenotic anterolaterally, the pterotic posterolaterally, the exoccipital posteriorly, and the basioccipital posteroventrally. The lateral external face of the prootic is more or less concave as it extends dorsolaterally from its ventral articulation with the parasphenoid to its articulation with the sphenotic and pterosphenoid. The prootic contains foramina for the complex of the fifth and seventh cranial nerves.

In medial view the prootic shape is complex (Figs. 5, 6). Ventrally, there is a broad medial extension which articulates synchondrally with the contralateral prootic; this broad extension forms the roof of the posterior myelodome. Posteromedially, there is a broad, deep concavity in which lies the anterior of the sacculus and its large otolith (sagitta). Dorsolaterally, there is a broad concavity in which lies the utriculus.

The pterotics are paired compound bones which lie on the posterolateral border of the skull (Figs. 3, 4, 6, 7). There are synchondral articulations with the prootic anteroventrally. On the dorsal surface of the skull, the pterotic has an anterior ramus which partially overlies the sphenotic; the medial border is con-

vex and broadly overlies the parietal (fitting into a shallow concavity on the dorsal surface of that bone). The dorsal anterior ramus is itself overlain by the dermosphenotic. A laterosensory canal extends along the dorsolateral pterotic surface and is partially enclosed by bone. The ventrolateral surface of the pterotic bears a long groove, the hyomandibular fossa. The ventral surface of the pterotic is concave.

The medial surface of the pterotic, which partially lines the cranial fossa, is primarily an ossification which contains the horizontal semicircular canal (Figs. 5, 6).

The posttemporal fossa lies in the posterior region of the neurocranium, near its dorsolateral border. The opening of the fossa is bordered medially by the epioccipital, and laterally by the pterotic. The dorsal wall and part of the medial wall of the fossa are formed by the parietal, the vertical and lateral walls by the pterotic. The fossa extends anteriorly to a point at about the mid-length of the pterotic, as viewed from dorsal aspect.

CIRCUMORBITAL BONES

The orbital bone series of *Diplophos* is well developed and heavily ossified (Fig. 8).

The supraorbital is a thin elongate bone which forms the anterodorsal border of the orbit. The bone lies lateral to the frontal and posterolateral to the olfactory fossa. The anteromedial border of the supraorbital forms a small portion of the border of the olfactory fossa. The dorsal surface of the supraorbital is concave as the bone spreads laterally out over the eye.

The antorbital is a wafer-like thin bone which lies anterior to the orbit; its dorso-posterior border usually forms the lateral border of the olfactory capsule. In some specimens, the antorbital slightly overlies the maxilla. The antorbital may lie somewhat anteriorly offset from the

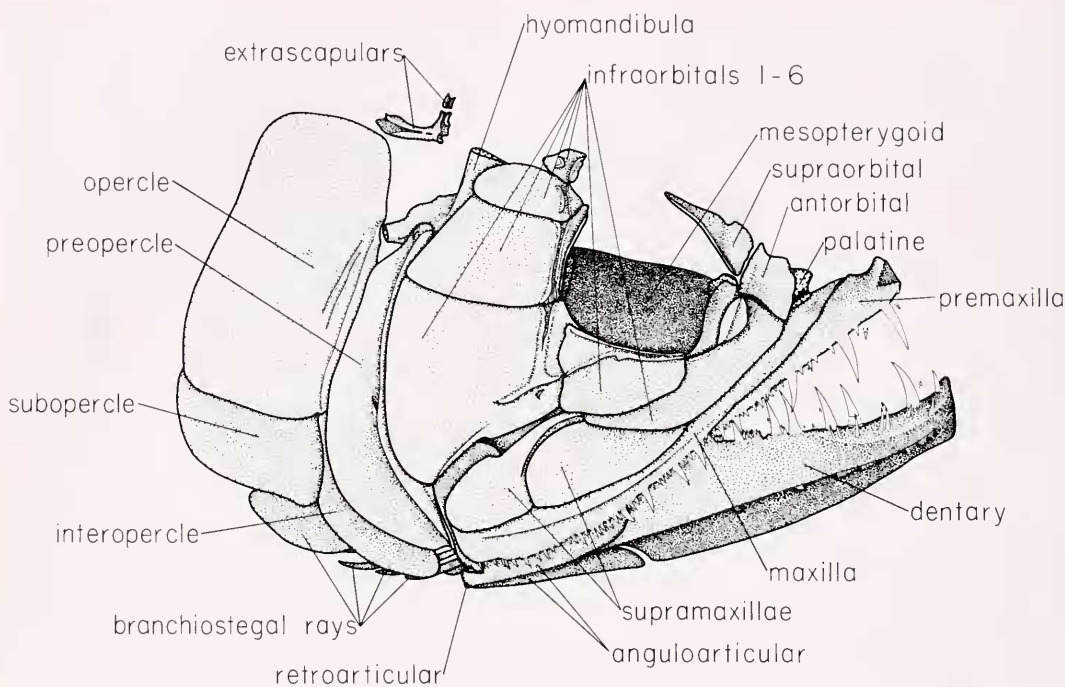


Figure 8. Suspensorium and infraorbital bone series of *D. taenia* (USNM 206614; 171.0 mm SL), lateral view.

supraorbital and the first infraorbital (IO1), so may be excluded from the anterior border of the orbit.

Infraorbital 1 lies along the anteroventral border of the orbit. There is a small sensory canal on the dorsal border, anteriorly. Anteriorly, the dorsal border is concave and follows the rim of the orbit; more posteriorly, the dorsal border becomes gently convex. The ventral border is more or less convex. Posteriorly, IO1 lies medial to IO2.

Infraorbital 2 forms the ventral border of the orbit. There is a laterally-projecting bony lamella along the dorsal border of IO2. Anteriorly, an open sensory canal extends just ventral to the lamella, then, just posterior to the mid-length of the bone, the canal extends posteroventrally to meet the canal on IO3. The ventral border of the thin bony lamella of IO2 is more or less convex. The posterior border of IO2 is slightly convex dorsally, between the dorsal border of the bone and

the sensory canal; ventral to the sensory canal, the border may be more or less posterior to IO1 and the anterior portion of IO3.

Infraorbital 3 is the largest of the infraorbital series. Anterodorsally, its border forms a portion of the orbital rim; posteriorly, the bone covers much of the "cheek" area and the adductor mandibulae muscles. The ventral border of IO3 is slightly convex anteriorly; more posteriorly, there is an abrupt ventral angle, and the ventral border is more deeply concave (this is dorsal to the area where the supramaxilla abuts IO3). The posterior border of IO3 is broadly convex and is tightly bound to the preopercle. The dorsal border of IO3 underlies IO4 and is gently concave. There is a sensory canal on IO3 which may be open or partially open and which consists of a vertical canal, an anterior canal, and one or two small, short, posterior canals.

Infraorbital 4 lies posterior to the orbit,

forming part of its posterior border. Anteriorly, IO4 has a well-developed sensory canal, nearly enclosed, which angles dorsally and slightly posteriorly, and is contiguous with the canal on IO5. The anterior border has a laterally-projecting flange, which is anterior to the sensory canal. The anterior and dorsal borders of IO4 are slightly concave; the ventral and posterior borders are slightly convex. The dorsal border lies medial to IO5, and the ventral border lies lateral to IO3.

Infraorbital 5 is smaller than IO4; it is more or less oblong in shape. The bone is excluded from the orbit by IO4. A small, open sensory canal lies in the anterior region of the infraorbital. The ventral border lies lateral to IO4; a small segment of the dorsal border is medial to IO6.

Infraorbital 6 (dermosphenotic) is a small bone which lies dorsal to IO5. The bone articulates syndesmotically on the flat anterior surface of the pterotic and on the posterior surface of the sphenotic. In specimens of *D. taenia*, IO6 is a rather short bone in an anteroposterior axis, being bluntly triangular or oblong. In *D. maderensis*, IO6 is a more elongate bone, extending more posteriorly on the pterotic. In both species there is an open sensory canal in the anterior region of the bone.

NASALS

The nasals are paired bones which lie medial to and partially form the medial borders of the olfactory fossae (Fig. 2). The nasal is syndesmotically articulated with the dorsal surface of the rostrodermethmoid. The nasal is primarily an open bony canal which arches around the olfactory fossa.

UPPER JAW

The premaxillae are paired, toothed bones which form the anterodorsal border of the mouth (Figs. 4, 8). There is a small articular process anteriorly. The

premaxilla is slightly curved from dorsal aspect, is relatively broad anteriorly, and tapers to a blunt point posteriorly. Posterior to the articular process there is a deep concave facet, which serves as the articulation point with the maxilla. At the symphysis there is a slight concavity on the anterior surface of the premaxilla. On the posterior surface near the symphysis there is a concavity which serves as an attachment site for suspensory ligaments (see page 56). There are about five to eight fang-like teeth and numerous smaller teeth ankylosed to the ventral border of the bone (Type 1 of Fink, 1981).

The maxillae are paired bones which form the posterodorsal border of the mouth (Figs. 4, 8). Each maxilla is an elongate bone which is, from dorsal aspect, somewhat broad anteriorly and slender posteriorly. The medial surface of the anterior border of the maxilla is extended as a condyle. Ventral to the condyle is a convexity on which the anterior premaxillary-maxillary ligament attaches (Fig. 13). Anterolaterally near the symphysis, there is a shallow facet which articulates in the concavity on the posterior surface of the articular process of the premaxilla. For about half its length the maxilla articulates with the dorsomedial surface of the premaxilla and is toothless. At about the mid-length of the maxilla, the ventral border of the bone angles ventralward and becomes slightly convex to its posterior termination; in this area the ventral border bears numerous teeth (Fig. 8). The more anterior teeth are larger than those more posterior; all mature teeth have Type 1 attachment mode. The toothed area of the maxilla anteriorly meets the posterior extension of the premaxilla; thus, the upper border of the mouth is toothed along its entire length. At about the middle of the lateral surface along the tooth-bearing portion of the maxilla there is a small lateral lamella of bone (Fig. 8).

There are two pairs of supramaxillary bones. The anterior supramaxilla lies in

connective tissue dorsal to the anterior toothed portion of the maxilla and articulates with the dorsolateral surface of that bone (Fig. 8). The ventral border of the anterior supramaxilla is nearly straight or slightly convex. Anteriorly, the bone border is broadly convex. The dorsal border is slightly concave anteriorly and broadly convex posteriorly. The posterior border is broadly convex. The bone, in a dorsoventral plane, is much larger posteriorly than anteriorly. The dorsal and posterior borders lie lateral to, and attach by dense connective tissue to, the posterior supramaxilla.

The posterior supramaxilla is an elongate, thin bone that lies medial and posterior to the anterior supramaxilla and dorsal to the posterior area of the tooth-bearing portion of the maxilla (Fig. 8). Posteriorly, the ventral border of the posterior supramaxilla is more or less straight and in line with the same border of the anterior supramaxilla, articulating with the dorsolateral face of the maxilla. Anteriorly, the ventral border is deeply concave, roughly matching the curvature of the posterodorsal border of the anterior supramaxilla. The dorsal border of the posterior supramaxilla is convex anteriorly, then concave for a short distance, then posteriorly is convex to the posterior termination of the bone. Thus, the posterior supramaxilla has two portions: an anterior slender, curving ramus of bone and a more oblong posterior section. The anterior ramus bears a lateral facet into which articulates the posterodorsal border of the anterior supramaxilla (Fig. 8).

LOWER JAW

The dentaries are paired and are the tooth-bearing bones which form most of the ventral border of the mouth (Figs. 4, 8). From dorsal aspect, the main body of the dentary is more or less straight posteriorly, arching medially anteriorly. The dentaries are joined at the midline anteriorly by a strong syndesmotomic joint. The

main body of the dentary contains a deep median fossa for attachment of the adductor muscles (Fig. 4). Ventral to this main dentary body is a long bony flange which forms the ventral border for most of the dentary length.

The dorsal border of the dentary bears four to eight large fang-like teeth and numerous smaller teeth. Anteriorly there is a short outer row of five to nine slender teeth and an inner row of much larger caniniform teeth. Posteriorly the teeth are all more or less in a single row; here the small teeth are much smaller than the large caniniform teeth. All teeth have Type 1 attachment mode. The postero-medial border of the dentary is deeply concave and is the medial border of the mandibular fossa; the posterolateral border of the dentary is also concave, but the concavity extends anteriorly less than half the distance of the medial border.

The anguloarticulars are paired bones which form the major posterior portion of the mandible (Figs. 4, 8). The bone is of complex shape. Anteriorly the bone lies medial and dorsal to the lateral and ventral walls of the mandibular fossa of the dentary. The ventral border of the anguloarticular extends anteriorly to a point just anterior to the medial border of the fossa on the dentary; in the region dorsal to the ventral flange of the dentary, the ventral border of the anguloarticular is straight, but posterior to that area the anguloarticular has its own ventral flange (Fig. 8). The dorsal anguloarticular border is concave anteriorly (Fig. 8) and slightly convex posteriorly. The posterior border is deeply convex dorsally and deeply concave ventrally, where there is an articular facet for the quadrate. The inner wall of the anguloarticular forms a shallow fossa, continuous with that of the dentary; posteriorly there is a medial wall of the fossa.

The retroarticular is a small cap of bone which articulates tightly against the posteromedial apex of the anguloarticular (Figs. 4, 8).

Meckel's cartilage is a slender rod of cartilage which extends along the floor of the mandibular fossa from a small condyle on the anguloarticular at the ventral border of the inner wall of the fossa (Fig. 4) to near the symphysis in the main body of the dentary.

PALATINE ARCH AND DORSAL PORTION OF THE HYOID ARCH

The quadrates are paired bones that form the ventral portions of the suspensoria, to which the mandible articulates (Fig. 4). The quadrate is more or less triangular, with a ventral apex in the form of an articular facet for the anguloarticular. The anterior border of the quadrate is more or less straight and extends in an anterodorsal direction. The anterior border lies lateral to and articulates by connective tissue with the posterior border of the ectopterygoid. The dorsal border of the quadrate is slightly convex and has a synchondral joint with the metapterygoid bone. The posterior border of the quadrate proper is more or less straight and is nearly vertical or canted slightly dorsoposteriorly. The posterior quadrate border has a tight syndesmotic joint with the symplectic, which lies against it. Posterolateral to the posterior quadrate border is a slender bony flange which has a slightly convex border, and which extends from near the dorsalmost point of the quadrate to near the articular facet.

The ectopterygoid bones form the posteroventral borders of the palatine arches (Fig. 4). The ectopterygoid is an elongate bone which extends from near the articulation of the quadrate and the anguloarticular to a point near the anterior articulations of the palatine with the neurocranium. The ventral border of the ectopterygoid is very broadly concave. The anterior border has a tight syndesmotic joint with the posterodorsal surface of the palatine bone and is tapered anterodorsally to a blunt point. The dorsal border of the ectopterygoid is more or

less straight or slightly concave. The posterior border is somewhat variable among individuals and may be slightly convex ventrally and rather deeply concave dorsally, or it may be slightly concave, with a convexity near the dorsal border (Fig. 4). Along the dorsal border of the ectopterygoid there are two bony flanges, one which extends anterolaterally and one which extends medially along the entire dorsal border of the bone. Within the concavity formed by these flanges is the articular surface for the synchondral joints with the mesopterygoid anteriorly and the metapterygoid posteriorly. The anterolateral flange of the ectopterygoid lies lateral to the mesopterygoid articulation and ventral to the metapterygoid articulation. The medial flange of bone lies medial or ventromedial to the mesopterygoid and medial to the metapterygoid (Fig. 4).

The palatine bones form the anteroventral borders of the palatine arch (Figs. 4, 13, 14). The palatine can be seen to consist of two condyles which articulate with the neurocranium and a posterior ramus which extends ventral to the ectopterygoid. The anterior condyle articulates with the ethmoid cartilage in the area of the prenasal process. This condyle is more or less triangular in cross section and has a large cartilaginous tip. The ventral border has a small edge which has one to four recurved teeth; this toothed ridge is slightly medial to the tooth-bearing portion of the posterior palatine ramus. The posterior condyle lies posteromedial to the anterior condyle and articulates with the ethmoid cartilage in the region of the lateral ethmoid (Fig. 4). This condyle is quite broad and has a concave dorsal surface. The medial bony border is deeply convex from dorsal aspect; the medial cartilaginous border extends medially to near the anteromedial border of the mesopterygoid in small specimens and forms a synchondral joint with that bone in large specimens. Posteriorly, the posterior condyle overlaps

the mesopterygoid, which articulates in a shallow facet on the ventral palatine surface. The posterior palatine ramus extends posteriorly about one-quarter the anterior length of the ectopterygoid; the ramus tapers to a blunt point near the ventral border of the ectopterygoid. The ventrolateral border of the palatine bears a row of small recurved teeth; the anterior teeth are larger than those more posterior.

The mesopterygoids are paired bones which form the largest part of the dorsal wall of the palatine arch (Fig. 4). The dorsal two-thirds of the bone forms a concave "cup" which forms the medial wall of the orbit. The anterodorsal border of the bone is more or less straight or slightly convex anteriorly. The anterior ventral border is slightly concave at the articulation point with the palatine in the region of its condyle. The joint with the palatine is syndesmotic. The anterior border of the mesopterygoid lies ventromedial to the palatine condyle; in some specimens there is an anterior extension of the mesopterygoid which articulates in a facet on the ventral surface of the palatine condyle. The ventral border of the mesopterygoid tightly articulates with the ectopterygoid, as described above; the ventral border of the mesopterygoid lies lateral to the border of the ectopterygoid. The posterior border of the mesopterygoid is concave dorsally, and near its midpoint there is a posterior extension which extends under the medial surface of the metapterygoid; ventral to this extension, the posterior border may be slightly concave or slightly convex; the posterior mesopterygoid border is tightly articulated with the anterior of the metapterygoid. At the medialmost part of the mesopterygoid, ventral to the orbit, is a patch of numerous small teeth.

The metapterygoid bones are paired and form the posterodorsal wall of the palatine arch (Fig. 4). The anteroventral border is broadly convex, articulating synchondrally with the quadrate postero-

ventrally and the ectopterygoid anteroventrally, and syndesmotically with the ectopterygoid anteriorly. There is a small anterodorsal ramus of the metapterygoid that extends somewhat lateral to the main vertical axis of the bone; this ramus is continuous with a bony flange that extends somewhat medially as the dorsal and posterior borders of the mesopterygoid bone. At about the midpoint of the dorsal border there is a large dorsolaterally-projecting flange that reaches an apex as the posterodorsalmost point of the bone. The flange is continuous along the posterior border of the bone to its posteroventral apex. The medial flange articulates synchondrally with the antero-medial surface of the ventral body of the hyomandibula; the lateral flange articulates with or lies lateral to the lateral border of the ventral body of the hyomandibula. In *D. taenia* the dorsal border of the metapterygoid, represented by the medial flange, lies near or articulates synchondrally with the anterodorsal flange of the hyomandibula and is more or less straight or slightly convex posteriorly; there is a rather marked angle at the junction of the dorsal and posterior borders. In *D. maderensis*, the metapterygoid dorsal border lies ventral to the hyomandibular flange, and the dorsal border is convex and continuous with the posterior metapterygoid border.

The hyomandibulae are paired bones which serve to brace the palatine arch to the neurocranium posteriorly, and which also articulate with much of the opercular series (Fig. 4). The hyomandibula is broadest in the anteroposterior plane near its dorsal border. The main body of the bone, which is endochondral, becomes abruptly narrower ventrally, forming a single elongate ventral ramus which extends to a point near the ventral border of the metapterygoid bone. There is a large anterior bony flange on the hyomandibula for about half its length; for a description of the flange shape and relationships with the metapterygoid, see the

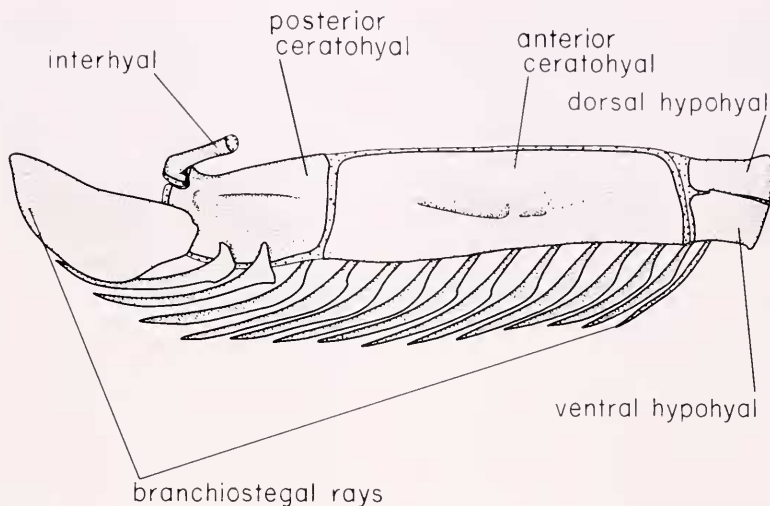


Figure 9. Hyoid arch, ventral portion, of *D. taenia* (USNM 206614; 171.0 mm SL).

description of that bone, above. On the posterior border of the hyomandibula there is a laterally-projecting bony flange which extends from near the dorsal border of the bone to near the ventral border at the apex of the elongate ventral ramus. At about one-third the distance from the dorsal border along the hyomandibula there is a large posteroventrally directed cartilage-tipped condyle for the diarthrodial articulation of the opercle. Small bony flanges extend from the dorsal and ventral borders of the condyle to the posteromedial hyomandibular border.

A small photophore lies in the integument near the ventrolateral surface of the articular condyle. The dorsal border of the hyomandibula articulates in a diarthrodial joint with the neurocranium in the hyomandibular fossa on the ventral surfaces of the sphenotic and pterotic bones. The anterior border of the hyomandibula articulates with the metapterygoid as described above under the latter bone. The ventral border articulates diarthrodially with the symplectic, the interhyal, and the posterodorsal border of the quadrate; in some specimens there may be a small diarthrodial articulation with the metapterygoid. The posterior hyomandibular border articulates syndes-

motically along most of its border with the anterior border of the preopercle.

The symplectic is a slender bone which articulates syndesmotically tightly against the posteromedial surface of the quadrate (Fig. 4). The bone is shaped like an elongate cone, with its small apex ventrally, and with its somewhat expanded dorsal border capped by a large bulbous cartilage body. The dorsal cartilage articulates anteriorly with the quadrate and metapterygoid, dorsally with the hyomandibular, and posteriorly with the interhyal.

VENTRAL PORTION OF THE HYOID ARCH

The interhyal is a rod-shaped bone which connects the ventral portion of the hyoid arch to the suspensorium (Figs. 4, 9). Dorsally there is a dome-shaped cartilage which articulates diarthrodially with the symplectic and hyomandibula. Ventrally the interhyal has a wide, cartilage-lined facet which articulates diarthrodially with the posterior ceratohyal bone.

The posterior ceratohyal forms about 20–25% of the length of the hyoid bar (Fig. 9). It is thin in cross section. In lateral view, the dorsal border is concave

posteriorly and straight anteriorly. The posterior border is composed primarily of the articular facet for the interhyal and consists of a deep cartilage-lined dorsal concavity; ventral to the articular surface the border is deeply convex and is continuous with the long convex ventral border. The anterior border is also broadly convex and diarthrodially articulates with the anterior ceratohyal. Four branchiostegal rays attach to the posterior ceratohyal; the posterior three articulate on the ventrolateral surface of the bone, the anterior ray on the medial surface very near the anterior ossified border of the bone.

The anterior ceratohyal is an elongate bone, also thin in cross section, which makes up the bulk of the hyoid bar (Fig. 9). In lateral view, its dorsal border is more or less straight or slightly convex; the posterior border is slightly convex and articulates synchondrally with the posterior ceratohyal; the anterior border is also slightly convex, and there is a large cartilage extension beyond the ossification which articulates diarthrodially with the dorsal and ventral hypohyals; the ventral border is slightly concave. Eight branchiostegal rays articulate with the ventromedial surface of the anterior ceratohyal in *D. maderensis*, nine in *D. taenia*.

The dorsal and ventral hypohyals are ossifications of a single cartilage block which lies anterior to the anterior ceratohyal (Figs. 9, 10). The dorsal hypohyal is slightly concave dorsally; anterodorsally, there is an articular facet for the basihyal and for a ligament to the first gill arch; the anterior border of the bone ventral to the articular facet is straight. The ventral border is more or less straight, becoming convex posteriorly; this convexity is continuous with the slightly convex posterior border of the bone. Ventral to the ventral border of the dorsal hypohyal is a cartilaginous area; ventral to that area is the straight or slightly convex dorsal border of the ventral hypohyal (in

large specimens the cartilaginous area is so small that there is a tight synchondral joint between the bones). The posterior border of the ventral hypohyal is straight or slightly concave; the ventral border is slightly concave; the anterior border is more or less straight. In the medial surfaces of both hypohyals is a continuous deep concavity which lies in a dorso-ventral plane; this concavity is the articulation point for the basibranchial of the first gill arch. One branchiostegal articulates with the posteromedial surface of the ventral hypohyal in *D. maderensis*, two in *D. taenia*.

The basihyal articulates with the anterodorsal and anterior borders of the basibranchial of the first gill arch, medial to the dorsal and ventral hypohyals (Fig. 10). Anteriorly the basihyal consists of a large rounded dome of cartilage with a dorsal perichondral ossification. The ossification extends posteriorly along the dorsal surface of the basibranchial and is somewhat wider laterally than the anterior ossified portion. There is a small tooth patch of small recurved teeth on the dorsal surface of the posterior bony portion of the basihyal. Basihyal morphology in *Diplophos* was illustrated by Weitzman (1974, Fig. 75B).

The urohyal is a single elongate median bone which lies ventral to the gill arches. The anterior portion of the urohyal is a well-developed condylar area which forms the anterodorsal apex of the bone. In large specimens this area is joined to the rest of the urohyal by a slender "neck." Anterodorsally on this condylar portion there are short bilateral rami which serve as attachment sites for ligaments extending to the anterior borders of the ventral hypohyals; anteroventrally, there is an attachment site for a ligament extending to the anteroventral border of the ventral hypohyal. Posterior to the articular condyles, the dorsal urohyal border is very broadly convex. In large specimens the dorsal border is represented by a median flange of bone

which extends beyond the more heavily ossified body of the bone. In smaller specimens, the anterior border extends ventrally from the articular condylar area as a more or less straight line which then becomes convex and continuous with the broadly convex, slightly irregular, ventral border; in larger specimens the anterior border is convex and continuous with the ventral border. The ventral border meets the dorsal border at the dorsoposterior apex of the bone. The urohyal is, for most of its area, a very thin plate of bone; both the anterior and dorsal urohyal borders are more heavily ossified than the rest of the urohyal except for the anterodorsal condylar area.

OPERCULAR BONES

The preopercle is the anterior bone in the series (Figs. 4, 8). In *D. maderensis* examined, the main body of the preopercle is an enclosed bony sensory canal which has a more or less dorsoventral main axis; ventrally, this bone angles anteroventrally. The anterior preopercular border is more or less straight dorsally; in the region of the posteroventral border of the metapterygoid, the preopercular border is composed of a bony flange which curves slightly concavely and articulates syndesmotically against the posterior border of the quadrate. Extending from the posterior border of the enclosed canal are two flanges, one posterior and one posterolateral; both flanges have their dorsal borders near the posteroventral border of the dorsal opening of the canal. Dorsally, the posterior flange is more or less straight or slightly concave; ventrally, the border is broadly convex. The posterolateral flange is smaller than the posterior flange and is slightly convex dorsally and broadly convex ventrally. The preopercular canal has its ventral opening at about the midpoint of the broadly convex area of the posterolateral flange.

The preopercle in *D. taenia* specimens

examined (all of which are larger than the *D. maderensis* examined) has no fully enclosed bony canal. The posterior and posterolateral flanges extend as in *D. maderensis* but are not interconnected by a posterior bony wall. There may be a small connection between the two flanges at about the mid-length of the preopercle (see Fig. 8).

In all specimens examined, the posterior borders of infraorbitals 3 and 4 articulate lateral to the posterolateral preopercular flange. The posteromedial border of the posterior flange articulates tightly against the opercle.

The opercle is the largest bone in the opercular series (Figs. 4, 8). The bone has a slightly convex dorsal border. The anterior border is somewhat concave dorsal to the articulation with the hyomandibula, and somewhat convex ventral to that point. The articular facet lies at a distance from the dorsal border of about 20–25% of the dorsoventral length of the bone. On the medial opercular surface, a ridge of bone extends posteroventrally from the articular surface; a second ridge follows the anterior border of the opercle. On the lateral surface of the opercle there is a small bony flange extending laterally, just posterior to the anterior border of the bone; this flange articulates against the posterior border of the preopercle. The ventral opercular border is slightly convex or more or less straight. The posterior opercular border is slightly convex dorsally and ventrally, with a concave area between the convexities.

The subopercle lies ventral and medial to the opercle (Figs. 4, 8). The bone is somewhat rectangular in shape, and about equal in anteroposterior length to the opercle. The anterodorsal corner is a small area of reinforced bone; from that area, the anterior border is somewhat S-shaped, concave dorsally and convex ventrally. The ventral border is more or less straight anteriorly, broadly convex posteriorly and continuous with the posterior border. The dorsal border is some-

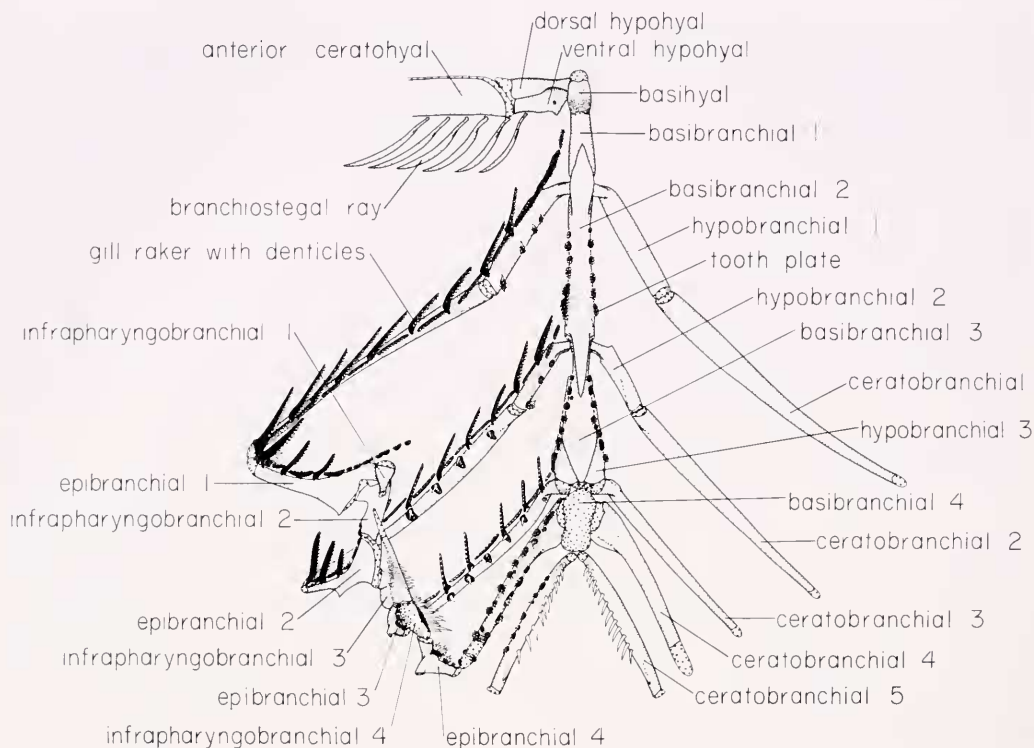


Figure 10. Branchial apparatus of *D. taenia* (USNM 206614; 171.0 mm SL), dorsal view; portions of right side removed; left side spread laterally. Tooth plates in black.

what concave anteriorly and straight posteriorly. About 20% of the dorsal area of the subopercle lies medial to the opercle. The anterior border lies medial to and articulates with the interopercle.

The interopercle is an irregularly-shaped bone which lies anterior and anteroventral to the subopercle (Figs. 4, 8). Ventrally, the anterior border is slightly concave, with an indentation in the area near the interhyal bone; dorsally, the anterior border is convex. The posterior border is convex along its articulation with the subopercle and then broadly convex to the anteroventral apex of the bone. The interopercle articulates by connective tissue to the medial surface of the preopercle (see Fig. 4).

BRANCHIAL APPARATUS

The infrapharyngobranchial of the first arch is a rod-shaped bone which is relatively thin in cross section dorsally, and larger and almost triangular in cross section ventrally. It articulates dorsally with the prootic, near the midpoint of that bone (Fig. 4), and ventrally diarthrodially with the anterolateral border of the epibranchial of the first arch (Figs. 10, 11). There are no tooth plates associated with infrapharyngobranchial 1. The bone lies, in lateral view, in a more or less dorsoventral plane and suspends the gill apparatus from the neurocranium.

Infrapharyngobranchial 2 is a bone nearly twice the length of infrapharyn-

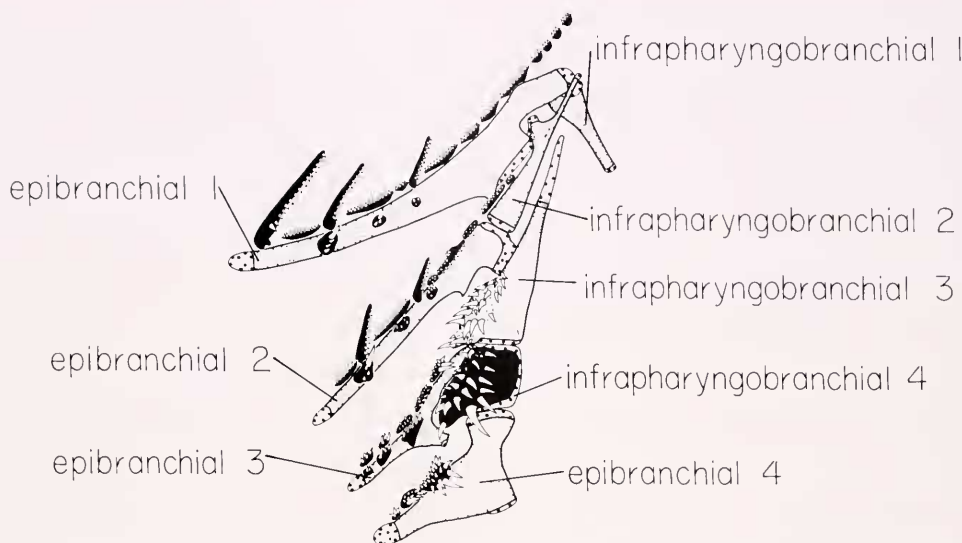


Figure 11. Dorsal portion of branchial apparatus of *D. taenia* (USNM 206614; 171.0 mm SL). Tooth plates in black.

gobranchial 1 (Figs. 10, 11). It consists of a long slender, anteriorly projecting ramus, cartilage-capped, which reaches a point equal to the anterior extent of epibranchial 1 and articulates diarthrodially with that bone. Posterior to the elongate anterior ramus is a vertical ramus which forms an uncinat process; it, too, is cartilage-capped, and it articulates with a concavity in the anterodorsal surface of epibranchial 1. Posteriorly, infrapharyngobranchial 2 is broader and articulates diarthrodially with epibranchial 2. There is an elongate tooth patch along the posterolateral border of the second infrapharyngobranchial. The *in vivo* alignment of the bone is anteromedial to posterolateral. There is a slender bony flange, convex from dorsal aspect, which extends along the medial border of the bone from the anterior portion of the anterior ramus to the posteromedial border of the bone near its articulation with the epibranchial.

Infrapharyngobranchial 3 is somewhat longer than infrapharyngobranchial 2 and lies posterior and medial to that bone

(Figs. 10, 11). There is an elongate anterior ramus whose ossification border is near the level of the dorsal uncinat process of infrapharyngobranchial 2 and which extends, as cartilage, to articulate near the anteromedial border of infrapharyngobranchial 2. At about the mid-length of the bone, there is a large concave articular facet laterally, in which the epibranchial of the second arch tightly articulates diarthrodially. Posterior to that point, the bone becomes much wider, carrying on its ventrolateral surface a large bony tooth plate with numerous Type 3 teeth (Fink, 1981). The tooth plate is fused to the infrapharyngobranchial and extends posterolaterally somewhat beyond the border of the infrapharyngobranchial proper. The teeth are fairly large, much larger than those on the small tooth plate associated with infrapharyngobranchial 2. The posterior border of infrapharyngobranchial 3 is more or less straight or slightly convex and articulates diarthrodially with infrapharyngobranchial 4 for most of its width and laterally with the dorsal extension of the

epibranchial from the third gill arch. There is a wide bony flange extending from near the anterior ossification border of the anterior ramus, medially to near the posteromedial border of the infrapharyngobranchial.

Infrapharyngobranchial 4 is an almost cube-shaped cartilaginous body which diarthrodially articulates anteriorly with infrapharyngobranchial 3 and posteriorly with the epibranchial of the fourth arch (Figs. 10, 11). There is a large toothplate tightly bound to the ventral surface of infrapharyngobranchial 4; part of the ossification of this toothplate overlaps the lateral border of the cartilage and extends onto its dorsal surface; otherwise, the dorsal surface of the infrapharyngobranchial is unossified. The toothplate extends posterolaterally somewhat beyond the cartilage border. The teeth are Type 3.

The epibranchial of the first arch is an elongate bone (Figs. 10, 11). Anteriorly, it has an anterior-extending ramus, more or less round in cross section, which articulates with infrapharyngobranchial 1, as described above. Somewhat posterior to that region, there is an expanded dorsal condyle, capped with cartilage, followed posteriorly by a bony flange with a concave border. Anterior to the condyle is a deep concavity which extends forward to the base of the anterior extension of the anterior ramus. The dorsal uncinate process of infrapharyngobranchial 2 articulates in this concavity. Posteriorly, epibranchial 1 articulates diarthrodially with ceratobranchial 1. Along the anterior border of epibranchial 1 lie several small bony tooth plates (with Type 1 teeth) that extend from the skin of the roof of the mouth down onto the skin over the bone. There are three, anteriorly projecting, toothed gill rakers; in each space between the rakers lies an elongate, bony tooth plate with numerous small teeth.

Epibranchial 2 is quite broad anteriorly, in a dorsoventral plane (Figs. 10, 11). The anterior region of the bone is a very

large, complex cartilaginous surface which articulates anteriorly with infrapharyngobranchial 2 and medially with infrapharyngobranchial 3. There is a small dorsal flange of bone anteriorly. Posteriorly, the bone articulates with ceratobranchial 2. There are two or three gill rakers on the anterior border and elongate tooth plates between them.

Epibranchial 3 is much less broad anteriorly than epibranchial 2; there is a medially-curved anterior process which articulates diarthrodially between infrapharyngobranchials 3 and 4 (Figs. 10, 11). About midway along the length of the bone there is a dorsally-directed process, cartilage-capped, and a flange of bone ventral to that. Posteriorly, the epibranchial articulates diarthrodially with ceratobranchial 3. Epibranchial 3 has a toothplate medially, and about five or six smaller toothplates along its medial border.

Epibranchial 4 is quite large, very broad anteriorly, articulating diarthrodially across a broad cartilaginous joint with infrapharyngobranchial 4 (Figs. 10, 11). On the dorsal surface of the bone, at about its mid-length, there is a very large cartilage-tipped articular condyle, and posterior to that a large thin flange of bone that extends almost to the ventral border of the bone, where the bone articulates with ceratobranchial 4. There is a large, well-developed tooth plate on the ventral surface of epibranchial 4, at about its mid-length, and ventral to that another, smaller toothplate in the skin; lateral to that toothplate is another, much smaller.

The ceratobranchials are all much alike and will be described only briefly. The ceratobranchials form the major portion of the ventral part of the gill apparatus, articulating dorsally with the epibranchials and articulating ventrally with the hypobranchials (Fig. 10), excepting those of the fourth and fifth arches, which will be described below. On the dorsal border of the ceratobranchial of the first arch there

are seven toothed gill rakers, with small bony toothplates lying between them; there are one or two gill rakers which articulate in the area where the epibranchial and the ceratobranchial are joined. The second ceratobranchial carries five gill rakers, with a sixth lying in the area of articulation between the epibranchial and the ceratobranchial. Ceratobranchial 3 bears five gill rakers, also with bony tooth plates between them; another gill raker lies in the area of the epibranchial-ceratobranchial articulation. Ceratobranchial 4 bears numerous tooth plates on its anterior border, but no gill rakers. The fifth ceratobranchial bears numerous toothplates on its anterior border and small conical teeth on its dorsoposterior border; these teeth extend more anteriorly on the anterior portion of the bone.

The hypobranchial of the first arch is a relatively large bone that has a medially-directed anterior ramus which diarthrodially articulates in the area of articulation between the first and second basibranchials (Fig. 10). Posteriorly, it articulates diarthrodially with the ceratobranchial. Lateral to the medially-directed ramus of the hypobranchial there is a large articulation surface for a ligament (see below). The bone bears two well-developed toothed gill rakers and two or three tooth patches on its dorsal border. There are also two or three elongate tooth patches on the connective tissue covering the ligament which extends from the anterodorsal border of the hypobranchial to the anteromedial surface of the dorsal hypohyal. There are three or four small tooth plates on the ventromedial surface of the bone.

Hypobranchial 2 is shorter than hypobranchial 1. It also has a medially-directed ramus which has a large concave surface which diarthrodially articulates in the area of articulation between the first and second basibranchials (Fig. 10). Anterolaterally, there is a large articulation surface for a ligament (see below). The dorsal border of the hypobranchial bears

two large gill rakers and two toothplates. There is also a series of approximately eight or nine toothplates that are attached to the connective tissue that overlies the ligament which extends between the articular point on the anterolateral surface of the hypobranchial and the postero-medial surface of hypobranchial 1. There are two or three tooth patches on the posteroventral surface of the bone.

Hypobranchial 3 is tightly bound to the third basibranchial (Fig. 10). Anteriorly, the bone extends along the ventrolateral surface of the basibranchial and has a slender ossified ramus which continues as a cartilage body to attach to the posteromedial surface of hypobranchial 2; these bilateral rami nearly meet at the ventral midline and form a broad perichondral ossification laterally over basibranchial 3. More posteriorly hypobranchial 3 is tightly bound diarthrodially to the lateral and dorsal surfaces of basibranchial 3. The posterior border of hypobranchial 3 is deeply concave and articulates diarthrodially with the ceratobranchial of the third gill arch posteriorly and with basibranchial 4 medially.

As mentioned above, ceratobranchials 4 and 5 articulate directly with basibranchial 4.

The basibranchials are median, unpaired bones which are entirely toothless (although toothplates lie in connective tissues adjacent to basibranchials 2 and 3) (Fig. 10). The cartilage cores of basibranchials 1 and 2 apparently are continuous, forming a synchondrosis. The perichondral ossification of basibranchial 1 is more or less oval in cross section. The bone is elongate in an anteroposterior plane, with a broad surface anteriorly where the hypohyal articulates diarthrodially. The ventral borders of the ossifications do not meet, and cartilage is visible along the entire ventral border of the basibranchial. In the area between the ossifications of basibranchials 1 and 2 there are bilateral deep concavities in the

cartilage where the first hypobranchials articulate.

Basibranchial 2 is a perichondral ossification that surrounds the cartilage core (Fig. 10). The ventral bony border is more or less flat in a horizontal plane, with bilateral bony flanges extending from it. Dorsally, the ossification extends anteriorly to overlies the ossification of the posterodorsal surface of basibranchial 1; posteriorly, the bone extends over the ossification of basibranchial 3.

Basibranchial 3 is an elongate cartilage with perichondral ossification (Fig. 10). Ventrally, laterally, and posteriorly there are hypobranchial ossifications articulating with the basibranchial cartilage. Dorsally, there is an elongate perichondral ossification on the surface of the cartilage; anteriorly, this is overlain by bone from basibranchial 2. The cartilage of basibranchial 3 is not continuous with that of basibranchial 1 and 2, but articulates with it diarthrodially. Anterolaterally, basibranchial 3 articulates diarthrodially with the hypobranchials of the second arch.

Basibranchial 4 is a cartilaginous body articulating diarthrodially with basibranchial 3 anteriorly, with the ceratobranchial of the third arch anterolaterally, with the ceratobranchials of the fourth arch laterally, and with the ceratobranchial of the fifth arch posteriorly (Fig. 10).

RETRACTOR DORSALIS MUSCLE

The retractor dorsalis is a large, bilaterally paired, unsubdivided muscle with its origin on the ventral surfaces of the seventh to ninth vertebrae posterior to the neurocranium and its insertion on the posteromedial surface of the fourth infrapharyngobranchial. See Winterbottom (1974: 256) for a discussion of the nomenclature of this muscle.

LIGAMENTS OF THE SUSPENSORIUM

In *Diplophos* the interpremaxillary ligament is short and very thick, lying far dorsally on the short premaxillary artic-

ular process in a pronounced concavity on the medial premaxillary surface (Fig. 12A). The interpremaxillary ligament is unpaired, but all other ligaments described below are bilaterally paired. The premaxillary-rostrodermethmoid ligament is well developed and extends from the anterior border of the rostrodermethmoid, just lateral to the midline, primarily to the ventromedial surface of the contralateral premaxillary bone; some of the fibers extend to the ventromedial surface of the ipsilateral premaxilla (Fig. 12B). The anterior premaxillary-maxillary ligament extends from the ventral border of the maxilla to the posterior surface of the premaxilla on the articular process, lateral to the attachment site of the interpremaxillary ligament (Fig. 13). The posterior premaxillary-maxillary ligament extends from the dorsolateral surface of the maxilla, where that bone extends ventral to the premaxilla, to just ventral to the dorsal border of the premaxilla, at about the level of the second premaxillary fang (Fig. 14).

A premaxillary-rostral cartilage ligament extends from the posteroventral surface of the rostral cartilage to the posterior surface of the premaxillary bone near the attachment site of the anterior premaxillary-maxillary ligament (Fig. 13). The anterior palatamaxillary ligament extends as a short broad sheath from the anterolateral border of the cartilaginous palatine head to the dorsal surface of the maxilla near its anterolateral border, at about the dorsal midline of the bone. The medial palatamaxillary ligament extends from the anterolateral surface of the palatine teeth to the medial surface of the maxillary bone (Figs. 13, 14). The posterior palatamaxillary ligament extends anterolaterally from a point on the palatine bone posterolateral to the attachment site of the anterior palatamaxillary ligament (at about the level of the third to sixth palatine teeth) to the dorsolateral surface of the maxillary bone.

The antorbital-maxillary ligament extends anteroventrally from the postero-

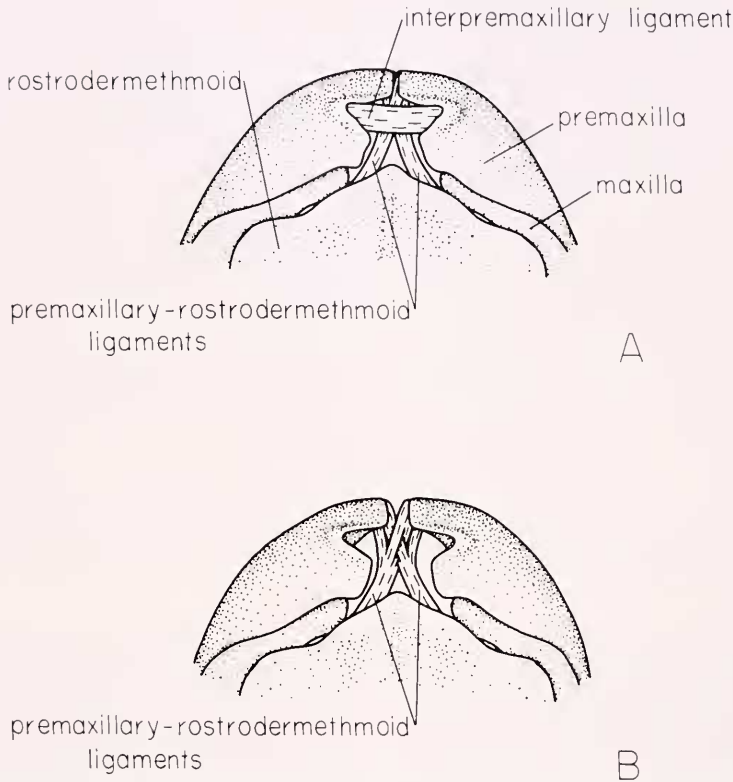


Figure 12. Anterior ligaments of suspensorium of *D. taenia* (USNM 206908; 184.3 mm SL), dorsal view. A. Interpremaxillary ligament in place. B. Interpremaxillary ligament removed.

ventral border of the antorbital to the maxilla, attaching just anterior to the anterior palatomaxillary ligament (Fig. 14).

The palatovomer ligament is broad, consisting of two primary bodies, one of which extends from a ventral prominence at the base of the anterior palatine tooth to the posterolateral border of the vomer; the second body extends between the posterolateral border of the vomer and the ventromedial edge of the palatine bone between the anterior palatine tooth and the anterior bony border of the palatine bone (Fig. 13). Both bodies of the palatovomer ligament are more or less continuous with one another. A well-developed palatine-lateral ethmoid (posterior surface) ligament extends from the dorsal surface of the palatine bone, at about the level of the medial palatomax-

illary ligament, to the posterior surface of the ethmoid bone (Fig. 14).

ADDUCTOR MANDIBULAE MUSCLES

In *Diplophos* the adductor mandibulae muscle is subdivided (Fig. 15A, B). The major, mostly lateral, division (A_2 , A_3) is a large, fan-shaped muscle with its origin on the ventrolateral surface of the hyomandibula and the anterolateral face of the preopercle; the muscle inserts, largely via a tendon, on the medial face of the anguloarticular near the posterodorsal border of the coronoid process. A few fibers have their origin medial to the smaller adductor division described immediately below; some anterior fibers insert on the primordial ligament (see below and Fig. 15B). The smaller, medial,

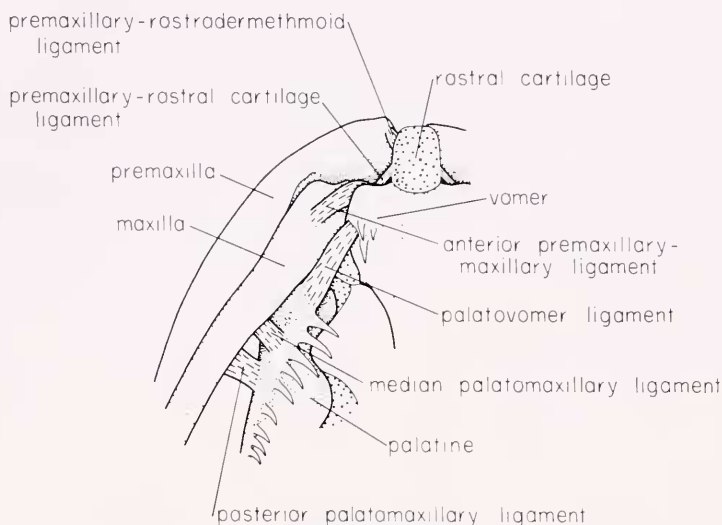


Figure 13. Ligaments of the suspensorium of *D. taenia* (USNM 206908; 184.3 mm SL), ventral view; maxilla and premaxilla spread slightly laterally; teeth of those bones not depicted.

division of the adductor consists of two sections, one dorsal and one ventral, each with origins on the posterolateral surface of the hyomandibula, quadrate, and metapterygoid (Fig. 15B). The dorsal section also has its origin in a raphe with the levator arcus palatini; it inserts on the dorsal border of the maxilla, just anterior to the mid-length of that bone; in small specimens there may be a fascia from the main muscle body to the insertion on the anterior supramaxilla and maxilla. The ventral section inserts on the primordial ligament. The dorsal attachment of the primordial ligament is on the lateral surface of the maxilla, anterior to the insertion of the dorsal section. The ventral insertion is on the lateral surface of the anguloarticular near its articulation with the quadrate. There is a tendon closely uniting the posterior supramaxilla to the primordial ligament. The fibers of the ventral section ventrally merge with those of the lateral division.

The fibers of the medial adductor muscles are virtually indistinguishable proximally, forming a continuous fan of mus-

cle, and in our specimens they can be identified only by their insertions.

The intramandibular division ($A\omega$) (not illustrated) of the adductor mandibulae has its origin on the anterior border of the tendon of the lateral division of the adductor and its insertion along the medial surface of the anguloarticular and dentary bones.

POSTCRANIAL AXIAL SKELETON

All counts except when otherwise designated are from *D. taenia*, USNM 206614. Counts for *D. maderensis*, USNM 186364, are given in parentheses.

The anterior element of the postcranial axial skeleton is the accessory neural arch (Fig. 5). Dorsally each arch element is unfused to its counterpart of the contralateral side. The joint between the arches is strongly bound by fibrous connective tissue and the dorsomedial apposing surface of each arch faced by cartilage. The entire arch encloses the dorsolateral surface of the spinal cord as it exits the cranium. The anterior and anteroventral

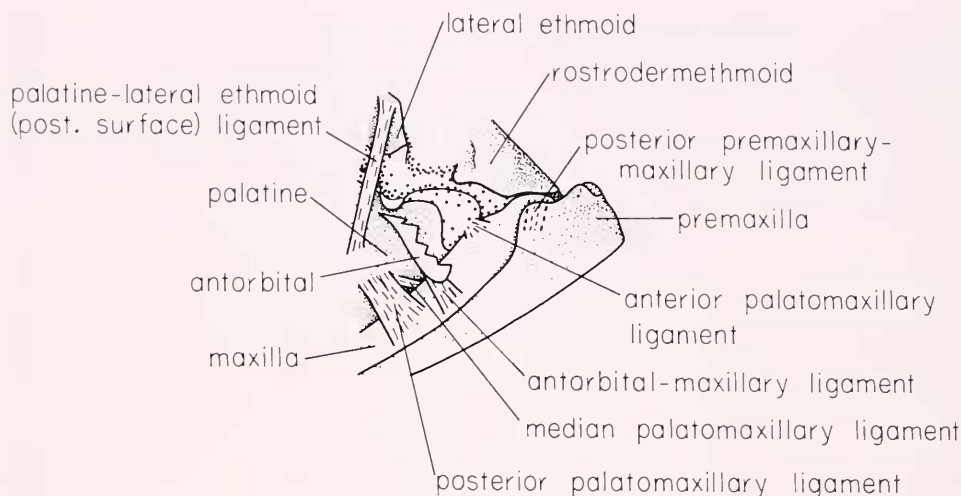


Figure 14. Ligaments of the suspensorium of *D. taenia* (USNM 206908; 184.3 mm SL), lateral view; antorbital bone partially removed; teeth not depicted.

borders of each arch element are bound by a sheet of strong fibrous connective tissue to the posterior arch-like face of the exoccipitals. This connective tissue sheet encloses the dorsal and lateral portions of the spinal canal and its contents. Ventrally, strong fibers of connective tissue bind each arch to the thick fibrous connective tissue between the anterior (first) vertebra and the exoccipital. Posteriorly, the border of the entire arch is joined by a sheet of connective tissue to the neural arch of the first vertebra. Successive neural arches are connected to each other in a similar manner.

There are 87 (63) vertebrae. Mukhacheva (1978) summarizes vertebral counts for *Diplophos* species. The first vertebra consists of an amphicoelous disc-shaped centrum associated with autogenous dorsolaterally-articulated neural arches and ventrally-articulated parapophyses. These structures are firmly bound by fibrous connective tissue to the relatively deep fossae which they fill. The neural arch of each side dorsally meets its counterpart in the same manner as the accessory neural arch. The neural arches are

anteroposteriorly broad along their dorsal border. The posterior border of the neural arch is fused with a short neural spine which is unfused to the spine of the contralateral side. Well ventrally on the posterior area of the neural arch at the anterior base of the neural spine is a slender epineural, which extends laterally and posterodorsally into the myocommata for the length of three to three and a half centra.

The parapophysis of the first vertebra bears a spinous process extending somewhat ventrally and posterolaterally. This process is continuous with Baudelot's ligament described below with the pectoral girdle. The postzygapophysis is located on the body of the centrum just posterior to the base of the neural arch. The first vertebra is separated from the exoccipitals and the centrum-like posterior facet of the basioccipital by a narrow space. The anterior border of the centrum is attached to the posterior exoccipital and basioccipital facets by thick fibrous connective tissue. The bodies of the first and second centra are closely approximated and their borders are bound together by

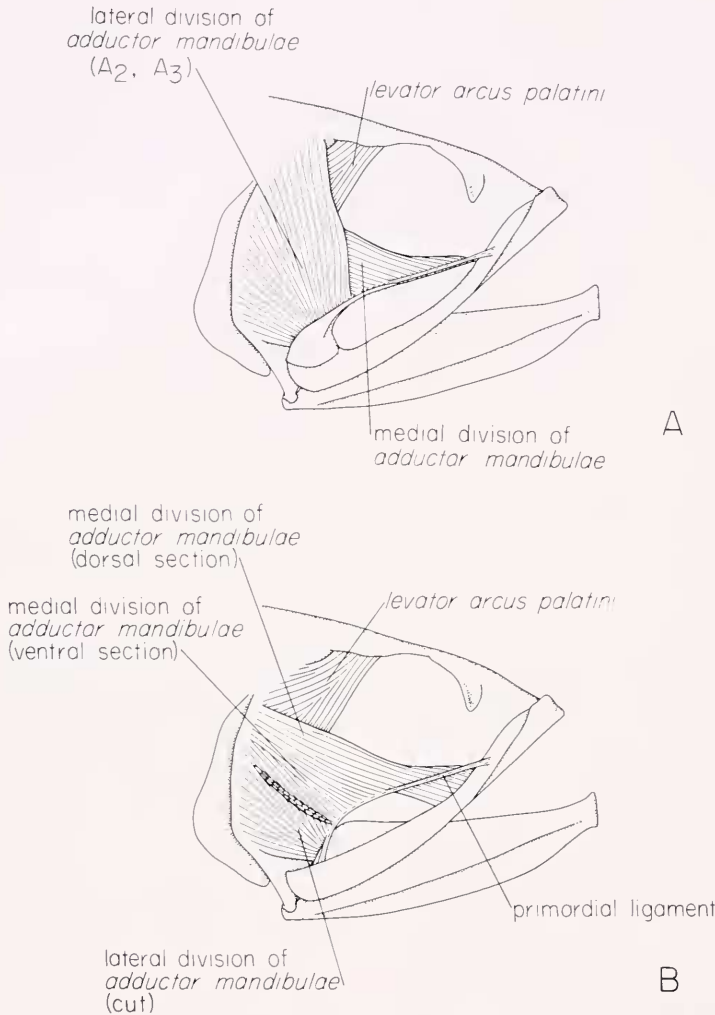


Figure 15. Adductor mandibulae muscles of *D. taenia* (MCZ 55469; 117.0 mm SL). A. Lateral division present. B. Lateral division removed to show underlying muscle.

strong fibrous connective tissues, as are those of all the successive centra.

The second vertebra is much the same as the first, but anteriorly the basal portion of its neural arch bears a prezygapophysis which has a medial face articulating with a posterolateral face of the postzygapophysis of the first vertebra.

The neural arches and spines of the second through the fourth vertebrae are similar in shape and articular relation-

ships to those of the first vertebra. The fifth (third) and successive vertebrae gradually diminish the broad dorsal border of the arches until by the eighth (sixth) vertebra these arches taper to their respective spines. The spines remain unfused until the 39th (30th) vertebra is reached. The spine of this vertebra inserts between the last two pterygiophores of the dorsal fin of *D. taenia*, but in *D. maderensis* it inserts between the

eighth and ninth pterygiophores. The second radial rod of the anterior dorsal fin pterygiophore passes between the 32nd (23rd) and 33rd (24th) vertebral spines. The last neural arch to directly bear an epineural is number 36 (29). Two (six) neural arches posterior to this bear short epineurals attached by moderately long ligaments. The last vertebra with a neural arch not fused to the centrum body is number 35 (29). The 36th (30th) vertebra has the neural arch entirely fused to the body of the centrum, as do the remaining centra, except the arches of the ural centra (see description of the caudal complex below).

The pattern of articulation between the dorsal post- and prezygapophyses described above for the first and second vertebrae is continued posteriorly through the entire vertebral column. However, only the first four or five (six or seven) vertebrae have the zygapophyses overlapping. In the more posterior vertebrae these processes approach each other with their respective anterior and posterior ends nearly abutting and bound to each other by fibrous connective tissue.

Parapophyses of the first through the 34th (27th) vertebrae are not fused to the centra. The 35th vertebra is the only vertebra to bear a fused parapophysis. There is no fused parapophysis in the *D. maderensis* examined.

The parapophysis of the second vertebra bears a short ventrolateral process which has fibrous ligaments extending into the associated ventral myocommata. The parapophysis of the fourth vertebra is the first to bear a pleural rib. This is attached to a short process of the parapophysis by fibrous connective tissue. The last parapophysis to bear a pleural rib is that of vertebra 35 (28). This vertebra marks the termination of the abdominal vertebrae.

The 36th (29th) vertebra bears a hemal arch and spine with the spines of each side ventrally fused, marking the beginning of the caudal vertebrae. The rib of

the 22nd (15th) vertebra is the first to bear an ossified epipleural and the rib of the 42nd (35th) vertebra is the last to bear such a structure. The tip of the hemal spine of the 38th (30th) vertebra lies just dorsal to the first anal-fin pterygiophore. Ventral zygapophyses are absent or nearly absent on vertebrae dorsal to the abdominal cavity. Abruptly posterior to or just dorsal to the posterior area of this cavity, narrow, small ridges of bone are located ventrolaterally on the anterior and posterior parts of the body of the centra. These ridges progressively enlarge posteriorly until near the mid-region of the caudal vertebrae they form small pre- and postzygapophyses that nearly abut each other. These processes are joined by rather weak fibrous connective tissue.

There are 16 (USNM 206614) or 17 (USNM 206908) supraneurals in *D. taenia* and 13 (USNM 180364) supraneurals in *D. maderensis*. The anterior supraneural in both species is an elongate, somewhat compressed rod of cartilage surrounded by a thin tube of bone except for its proximal and distal ends. This supraneural narrows near its mid-length, but anteriorly in this area has a thin blade-like ridge of bone. The proximal end of the anterior supraneural articulates with the anterior dorsal portion of the neural arch of the first vertebra. The distal end of the supraneural lies just beneath the skin at the midline of the back.

The remaining supraneurals in both species are small, slender cartilaginous rods surrounded by thin bone and lie between the neural spines of vertebrae 2 through 17 in *D. taenia*, USNM 206614.

CAUDAL SKELETON

The caudal skeletons of *Diplophos maderensis* (Fig. 16) and *D. taenia* are essentially the same except that *D. maderensis* has about 10–13 procurent dorsal-fin rays, *D. taenia* about 5–6. Only the caudal skeleton of *D. maderensis* is described below.

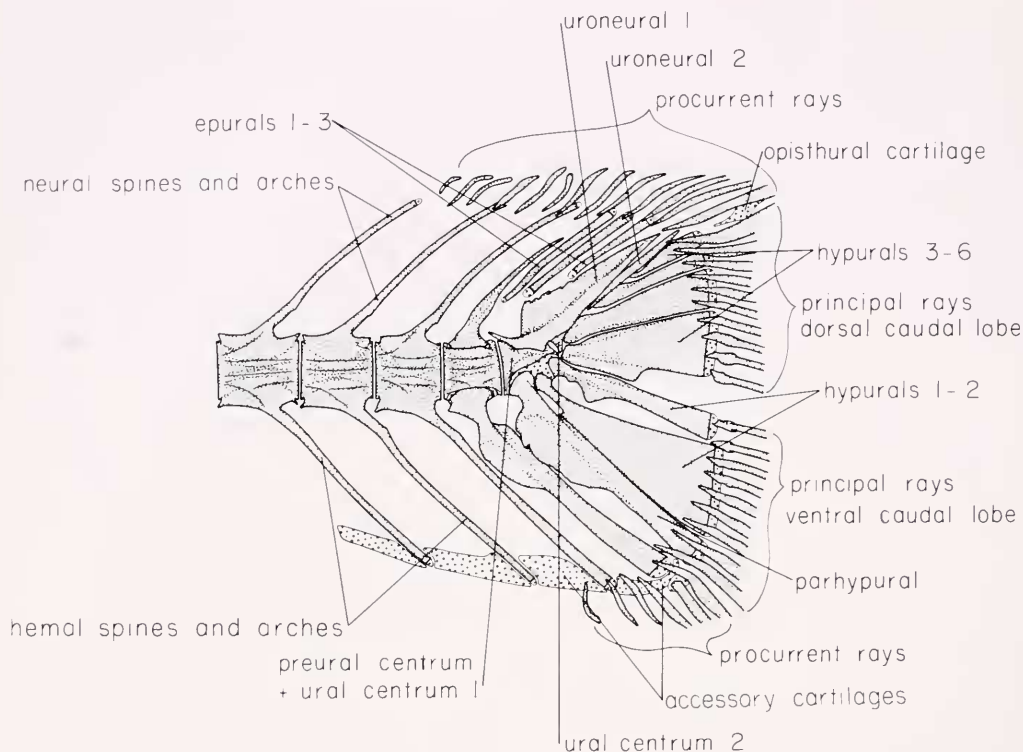


Figure 16. Caudal skeleton of *D. maderensis* (USNM 186282; 111.5 mm SL), lateral view.

A compound centrum consisting of the first preural and first ural centra posteroventrally supports the autogenous parhypural and first and second hypurals. Hypurals three through six are autogenous and separate from each other and lie posterior to the second ural centrum. There is an opisthural cartilage posterior to the sixth hypural, between the posterior dorsal procurent fin ray and the dorsal principal caudal-fin ray. The neural spine of the first preural vertebra and the first uroneural are autogenous, separate from the fused preural and ural centra below and the second ural centrum posteriorly. A splint-like second uroneural lies posterior to the first uroneural. There are three epurals dorsal to the first uroneural. The bases of the neural and hemal arches of the second preural centrum are autogenous, not fused to the centra as

they are in the more anterior caudal vertebrae. A urodermal and third uroneural are absent.

The five terminal caudal vertebrae support the caudal-fin rays but only the neural spines of the third through the fifth preural centra directly support dorsal procurent rays. The ventral procurent rays are primarily supported by cartilaginous radials associated with hemal spines borne by the second through the fourth preural centra. Large cartilaginous radials are found between the distal tips of the hemal spines that occur posterior to the termination of the base of the anal fin. There are 10 plus 9 principal caudal-fin rays.

VERTICAL FINS

In *Diplophos taenia* and *D. maderensis*, the basic osteological unit of the ver-

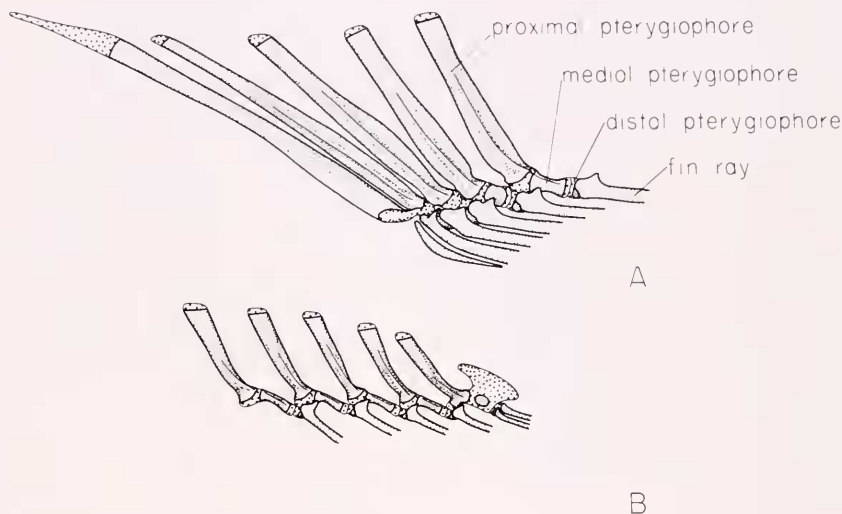


Figure 17. Anal fin skeleton of *D. maderensis* (USNM 186282; 111.5 mm SL). A. Anterior fin base. B. Posterior fin base.

tical fins is the pterygiophore series (Fig. 17A, B). Most of the fin base consists of pterygiophores with three sections: a proximal pterygiophore ossification, a medial pterygiophore ossification (both these ossifications over a single cartilage core), and a cartilaginous distal pterygiophore with bilateral perichondral ossification centers lying between the fin ray halves. The proximal pterygiophore is perichondrally ossified proximally and endochondrally ossified near its distal termination. The anterior and posterior portions of the fins have some modifications, as follows.

In the anal fin, the anterior two proximal pterygiophores are elongate rods which are fused together distally at their cartilaginous tips. The distal portion of the anterior rod of this pterygiophore is expanded bilaterally. The first and second fin rays articulate ventral to the distal cartilage; the second fin ray articulates with the anterior of the first (anterior) distal pterygiophore. Fin ray three lies ventral to the third pterygiophore series and

also articulates with the anterior cartilaginous distal pterygiophore. The fourth pterygiophore series consists of a proximal pterygiophore and a block-like medial pterygiophore; the fifth pterygiophore series has a more elongate medial pterygiophore, as do posteriorly successive pterygiophore series. The distal cartilage of the posterior pterygiophore is expanded posterodorsally and has small bilateral ossification centers; the posterior two fin rays share a single distal pterygiophore which articulates with the expanded medial cartilaginous pterygiophore.

In the dorsal fin of *D. taenia*, the anterior pterygiophore series is a tripartite structure that appears to be the fusion of two or three proximal pterygiophore elements. This compound structure is composed of an anterodorsally extended bony flange that in some specimens is rod-like dorsally, and two anteroventrally projecting rods, interconnected by a thin bony flange. Distally the anterior pterygiophore series is capped by a block of car-

tilage. A cartilaginous distal pterygiophore lies posterodorsal to the anterior proximal pterygiophore complex; the distal pterygiophore has bilateral ossification centers along its posterolateral surfaces. The first (anterior) and second fin rays articulate with the anterior distal pterygiophore. The distal cartilaginous cap of proximal pterygiophores two and three are more elongate than that of the first proximal pterygiophore; the posterior cartilaginous extension of proximal pterygiophore four has a medial pterygiophore ossification, as do posteriorly successive pterygiophore series, except for the posterior three to five.

Data on numbers of rays composing the vertical fins of *Diplophos* species are available in Johnson (1970) and Mukhacheva (1978).

PECTORAL GIRDLE

There are two extrascapulars, both consisting of tube bones and very little surface plate (Figs. 3, 4, 7, 8). The medial extrascapular is a short to moderately long open-tubed bone with its long axis nearly parallel with the posterior border of the parietal. A larger L-shaped lateral extrascapular has a long horizontal ramus and a short dorsomedial ramus which connects with the medial extrascapular. The lateral extrascapular is mostly an open tube, but in large adults it is closed superficially at the anteroventral junction of its two rami (Fig. 8). The sensory tube within the extrascapulars connects anteriorly with that of the pterotic and posteriorly with that of the posttemporal. Dorsally it exits from the medial extrascapular and extends a short distance in a groove on the external surface of the parietal. The extrascapulars of *D. maderensis* are almost exactly the same as those of *D. taenia*.

The posttemporal is well ossified and has blade-like anterodorsal and anteroventral principal rami (Fig. 4). The large dorsal ramus is articulated by a short

strong ligament to the posterodorsal process of the epioccipital. The narrower and shorter anteroventral ramus is attached by a strong ligament to the central knob-like process of the intercalar. A third, short posteroventral ramus is broadly attached to the dorsolateral surface of the supracleithrum by a short ligament. The posttemporal contains a laterosensory canal extending posteroventrally from the posterior, long ramus of the lateral extrascapular through the posteroventral ramus of the posttemporal. This canal is ventrally continuous with the laterosensory canal of the supracleithrum.

The supracleithrum is an elongate, fairly slender blade-like bone with the lateral face dorsally attached by a short strong ligament to the ventromedial articular surface of the posttemporal. The dorsal ramus of the cleithrum articulates with the medial surface of the supracleithrum. This articulation is extensive, including approximately the ventral half of the supracleithrum. The dorsal apex of the cleithrum lies immediately internal to the central portion of the posterior border of the supracleithrum. The supracleithrum bears a laterosensory canal along its posterior border for about one-third of its total length. Ventral to this canal, the entire posterior border of the supracleithrum continues as a groove, part of which bears a laterosensory canal. The laterosensory canal of the supracleithrum of *D. maderensis* is very similar to that of *D. taenia*.

The cleithrum is a large, complex bone which may be considered in three parts: a dorsal ramus, a body or central portion, and a ventral ramus. The dorsal ramus ends in a conical slender process attached as described above to the medial face of the supracleithrum. Ventrally the cleithrum widens anteroposteriorly to become a broad blade with a rugose or pitted lateral surface, especially anteriorly. The ventral portion of this blade abruptly turns anteriorly to become part

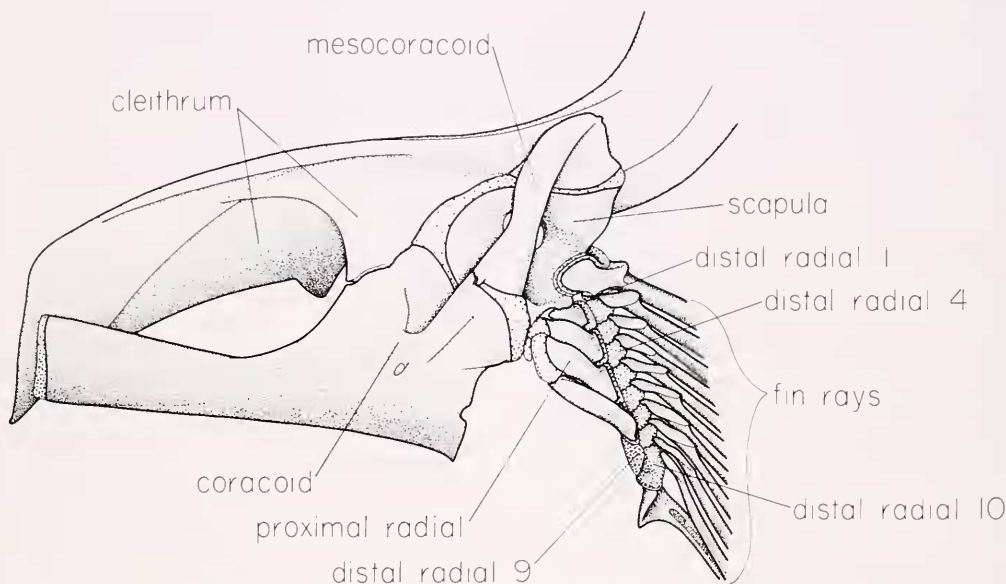


Figure 18. Pectoral girdle of *D. taenia* (USNM 206614; 171.0 mm SL), dorsomedial view.

of the body of the cleithrum which articulates with the pectoral girdle bones bearing the radials and fin rays (Fig. 18). A cross section near the mid-length of the blade-like portion of the dorsal ramus of the cleithrum is rounded anteriorly and abruptly narrower posteriorly. The posterior blade-like portion tapers to a thin edge posteriorly. The lateral wing of the cleithrum extends from the blade-like dorsal ramus of the cleithrum, continues as the lateral blade-like portion of the body of the cleithrum and extends forward as the main part of the anterior blade-like part of the cleithrum (Fig. 18). The body of the cleithrum bears a moderate sized medial wing which extends to contact the coracoid and scapula (Fig. 18). The anterior ramus of the cleithrum is a broad dorsoventrally placed sheet of bone which is anteriorly attached by ligaments to the cleithrum of the contralateral side and to the anterior coracoid ramus.

In some stomiiforms the major ligaments of the pectoral girdle become much modified, and for that reason par-

ticular attention is paid to them here. The ligaments of the posttemporal-cranial and the posttemporal-supracleithrum articulations were described above. The ligaments described below are numbered for ease of future reference. The supracleithrum and cleithrum are bound by a broad, very short ligament (1) which extends from the ventromedial surface of the supracleithrum to the dorsolateral surface of the cleithrum. This joint lies somewhat ventral to the region of the cleithrum where it narrows into a conical process.

Baudelot's ligament, ligament 2, extends posteriorly from the anterior vertebral centrum, passes medial to and wraps around the dorsal process of the cleithrum without attaching to it, and connects to the medial surface of the supracleithrum. This ligament is anteriorly attached to a ventrolateral extension of the parapophysis of the anterior vertebral centrum. This bony process extends nearly one-third to one-half of the distance from the centrum to the distal termination of the ligament.

The cartilaginous coracoscapular plate

and its ossifications in *Diplophos* are typical of many teleosts (see Starks, 1930) (Fig. 18). The cartilage body of the plate projects from the medial surface of the body of the cleithrum at its curvature. The coracoid bone, the anterior portion of the cleithrum, and the medial wing of the cleithrum surround a large coracoid aperture. The term coracoid aperture is used for this space because previous names for it, such as coracoid-cleithral foramen (Rendahl, 1933) and interosseus space (Starks, 1930) are inadequate to describe the various coracoid morphologies found in the stomiiforms. The coracoid cartilage is covered by well-ossified bony lamellae forming the coracoid bone. The coracoid is an L-shaped bone with a long anterior ramus meeting the cleithrum near its anteroventral termination. It has a broad lateral ramus contacting the medial cleithral wing. The anterior ramus terminates in cartilage. The coracoid articulates posterolaterally in a synchondral joint with the scapula. A short dorsolateral ramus is continuous with the cartilaginous base of the mesocoracoid. Anteriorly the coracoid and mesocoracoid contact each other in this area. The posteromedial ventral spinous process of the coracoid is short and blunt, not elongate as described for *Astronesthes niger* by Weitzman (1967b: 29). Both the anterior ramus and the short spinous process are flattened lateromedially.

The scapular ossification of *Diplophos* is composed of thin layers of bone, one dorsal and one ventral, which sandwich the posterolateral area of the coracoscapular plate (Fig. 18). The two bony layers meet and form a continuous bony surface along the posterior scapular border. There is an articular surface along the posterior scapular border for the proximal articular surface of the first pectoral-fin ray and proximal radial I (the lateral proximal radial, described below). The lateral portion of the scapula lateral to the scapular foramen extends vertically, and it articulates with the coracoid. Medially the

scapula extends in a plane that dips ventrally in a posteromedial direction. The scapula medially connects to the coracoid through a synchondral joint. The scapular foramen is entirely enclosed by bone.

The fully developed mesocoracoid of *Diplophos* is much like that of other teleosts as described by Starks (1930) (Fig. 18). The mesocoracoid is a tube of thin bone surrounding a rod of cartilage that extends from the coracoscapular plate at the posterior border of the coracoid and the scapula and laterally articulates with the medial surface of the cleithrum near the midpoint of the central curvature. A ventrolateral ramus of the lateral end of the mesocoracoid extends from its junction with the cleithrum as a sheet of bone over the medial surface of the cleithrum at its central curvature.

Herein, proximal radials are designated by Roman numerals (I–IV) and distal radials by Arabic numerals (1–10).

Proximal radial I is the most lateral of the proximal radials. It is proximally associated with the scapula and coracoscapular plate. Radials II, III, and IV are medially placed in succession. Radials II and III are in association proximally with the cartilaginous coracoscapular plate while radial IV is free of the plate.

Diplophos taenia has radial I short and with well-ossified bone around a central cartilaginous core (Fig. 18). There is exposed cartilage anterolaterally on radial I where it articulates with the medial border of the scapula and to a lesser extent with the cartilaginous border of the coracoscapular plate. There is also exposed cartilage distally on radial I where it articulates with distal radials 2 and 3. Medially, radial I articulates with radial II. Distally, radial I articulates with distal radial 2 and partially with 3. Radials II and III are much longer than radial I, with III being the longest. Both radials II and III have their proximal and distal ends of cartilage; they articulate proximally with the cartilage of the coracoscapular plate and distally with distal ra-

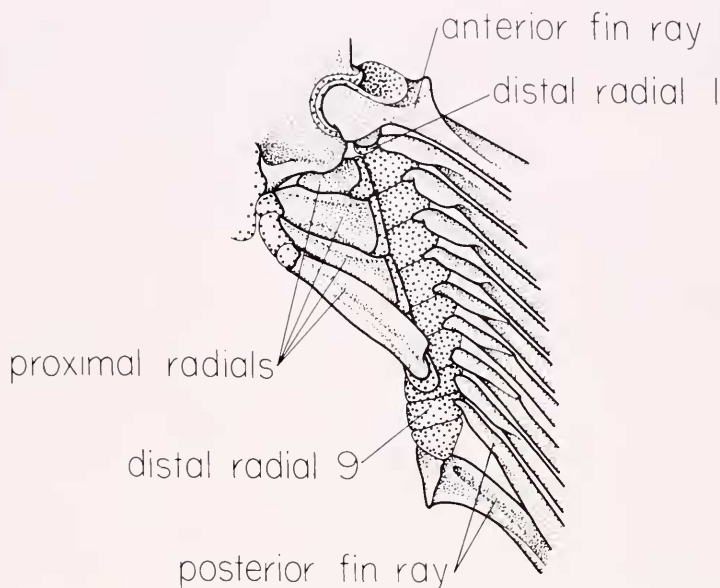


Figure 19. Pectoral radials and fin rays of *D. maderensis* (USNM 186282; 111.5 mm SL), dorsomedial view.

dials 3–4 and 5–6, respectively. Distally, radial IV articulates with distal radials 7–9; proximally, it articulates in an apparently immobile joint with radial III as part of a proximal radial plate between the coracoscapular plate and the distal radials (this morphology is also present in *D. rebaini*). Radial IV has a flange of thin, plate-like bone arching dorsomedially.

There are ten distal radials and ten fin rays in *D. taenia* (Fig. 18). The anterior distal radial (1) lies between the base of the ray halves of the large first pectoral-fin ray. The cartilage of this radial is firmly set on a short pedicel of bone of the dorsal ray half and articulates medially with distal radial 2 as well as with proximal radial I. The remaining nine distal radials are free of their respective fin rays and are articulated with them in a movable joint. There is one distal radial for each fin ray, and, except for radial 9, each ray has its dorsal half articulating with the dorsal anterolateral area of the distal radial and its ventral ray half articulating

with the ventral posteromedial area of the distal radial. Radial 9 lies dorsomedial to radials 8 and 10, which articulate directly with each other. (In *D. rebaini* distal radial 8, also the second from last, is likewise dorsomedial to its adjacent radials.)

The proximal and distal radials of *D. maderensis* (Fig. 19) differ from those of *D. taenia*. Proximal radials III and IV have separate cartilage cores, as in those of most teleosts. Proximal radial IV has a small ventral longitudinal flange, missing in *D. taenia*, and a somewhat smaller dorsal longitudinal flange than *D. taenia*. The relative plesiomorphic versus apomorphic nature of these flanges has not been determined. The ten distal radials of *D. maderensis* and their respective fin rays are arranged as in *D. taenia* except that distal radial 9 is in series with the other radials and bears the same relation to its fin ray as do radials 2 through 8. The articulation of proximal radial IV is directly with distal radials 6 through 8. Outgroup comparison indicates that the

condition of the distal radials in *D. maderensis* is plesiomorphic relative to that of *D. taenia*.

PELVIC GIRDLE

The pelvic girdle of *Diplophos* (Fig. 20) consists of two pelvic plates which are small relative to body size and are well ossified. Medially, the pelvic plates are bound closely together by connective tissue for most of their length, but they touch only at the anterior cartilaginous processes. They lie at an angle of about 45° to each other, with the apex dorsal. The anterior cartilaginous process is a short rounded extension of cartilage from the core of the anterior process just posterior. The anterior process is a long, narrow bony rod, cartilage-filled, which is slightly larger distally than proximally. The medial pelvic plate, a thin lamella of bone, extends along almost the entire medial border of the anterior process, and posteriorly joins the anterior border of the posterior plate; its medial border is slightly concave. A small lateral anterior plate extends between the proximal one-third of the anterior process and the lateral process. The anterior portion of the posterior plate consists of a short, medially directed bony rod, cartilage-filled; the medial surface of this rod is unossified. The anterior border of the rod lies at an angle of about 100–110° to the longitudinal axis of the pelvic plate. Posterior to this cartilage-filled rod, the posterior plate consists of a thin rugose lamella. In *D. taenia*, this lamella is endochondrally ossified to the posterior border of the basipterygium; in *D. maderensis*, a narrow cartilage border is present distally on this lamella. The postero-medial border of the posterior plate is deeply convex. The posterior border of the posterior plate joins the lateral process anterolaterally. The endochondrally ossified lateral process is short and broad and forms the lateral bony border of the basipterygium; lateral to it is the lateral

cartilaginous process, against which articulate the radials. There are three radials. The anterior two lie lateral to the lateral cartilaginous process, and the third, posterior, radial lies posterior to the cartilaginous process and lateral to the posterior plate. Radial 1, the anterior of the three, slightly smaller than the others, is an oval cartilage with dorsal and ventral ossification centers. Radial 1 lies between the ray halves of the first and second rays. Radial 2 is similar in structure to radial 1 and is associated with rays three through six. Radial 3 is a hemispherical cartilage anteriorly and is ossified posteriorly, tapering to a blunt, short process. This radial is associated with rays seven and eight. There are eight fin rays, all segmented with relatively short segments. Ray one is shortest and unbranched. The remaining rays are branched. Rays two and three are progressively longer, and rays four through eight progressively shorter, with ray eight about 75% of the longest ray (*D. taenia*).

The identity of actinopterygian pelvic girdle elements has been discussed by Stensio (1921, 1925) and Rosen *et al.* (1981), among others. Further investigations are needed to establish the homologies of actinopterygian and non-actinopterygian girdle elements, especially those of the pelvic plate proper and radial 3, which may be a metapterygial element.

RELATIONSHIPS OF THE STOMIIFORMES

At various times in the past, stomiiforms have been considered non-monophyletic, or monophyletic and related either to various primitive teleostean groups (protacanthopterygians, isospondyls, etc.) or to more derived teleosts (Eurypterygii of Rosen, 1973) (Fig. 21). Present evidence indicates that the group is monophyletic and corroborates a sister group relationship with the Eurypterygii.

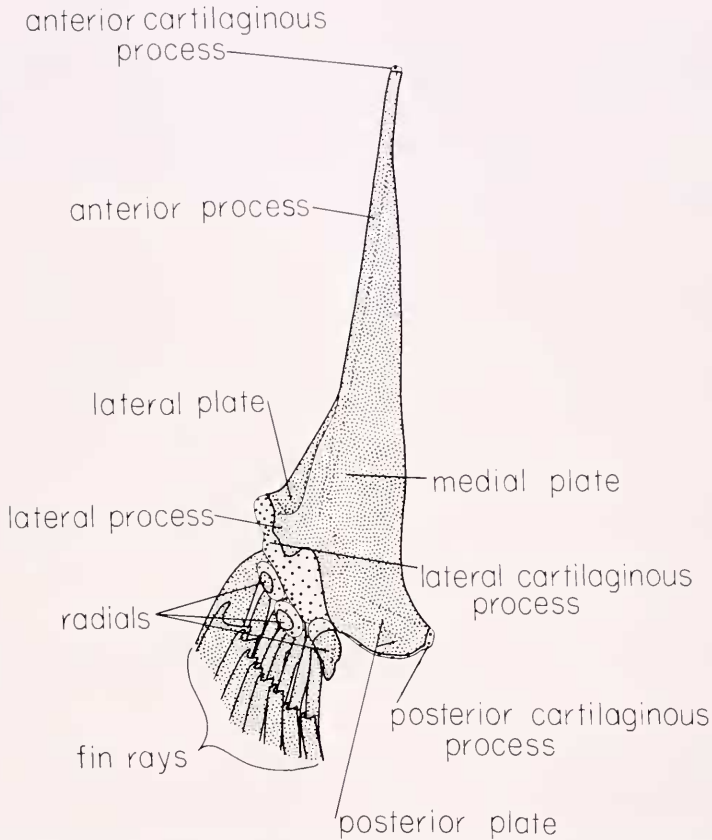


Figure 20. Pelvic fin girdle of *D. maderensis* (USNM 186282; 111.5 mm SL), ventral view; ventral fin ray halves removed proximally to show radials.

MONOPHYLY OF THE STOMIIFORMES

The morphological diversity of species now placed in the Stomiiformes has historically presented problems to systematic ichthyologists. The morphological differences between, say, *Argyropelecus* (see Weitzman, 1974, Figs. 11 and 12; Schultz, 1964, Fig. 64) and *Malacosteus* (see Morrow, 1964b, Fig. 144) confounded many early workers and led them to place various genera with groups now removed to other positions in our hypotheses of teleostean phylogeny. Most diagnoses of the group have included the presence of photophores and a combination of other features which are distributed widely among primitive teleosts (see Regan, 1923; Morrow, 1964a; Weitz-

man, 1967a; and our discussion concerning Greenwood *et al.*, 1966, below). So far as we are aware, the monophyly of the Stomiiformes has never been explicitly documented by characters unique to the group. The Stomiiformes can be diagnosed by the presence of the following characters:

1) Photophores with a structure unlike that of other teleosts. Bassot (1966, 1970) has described stomiiform photophores histologically and found that they are composed primarily of two cell types, designated by him as A and B. Type A cells, typified in part by the well-developed endoplasmic reticulum, apparently produce the luminescent product (see Herring and Morin, 1978). More recent works on the histology of stomiiform light

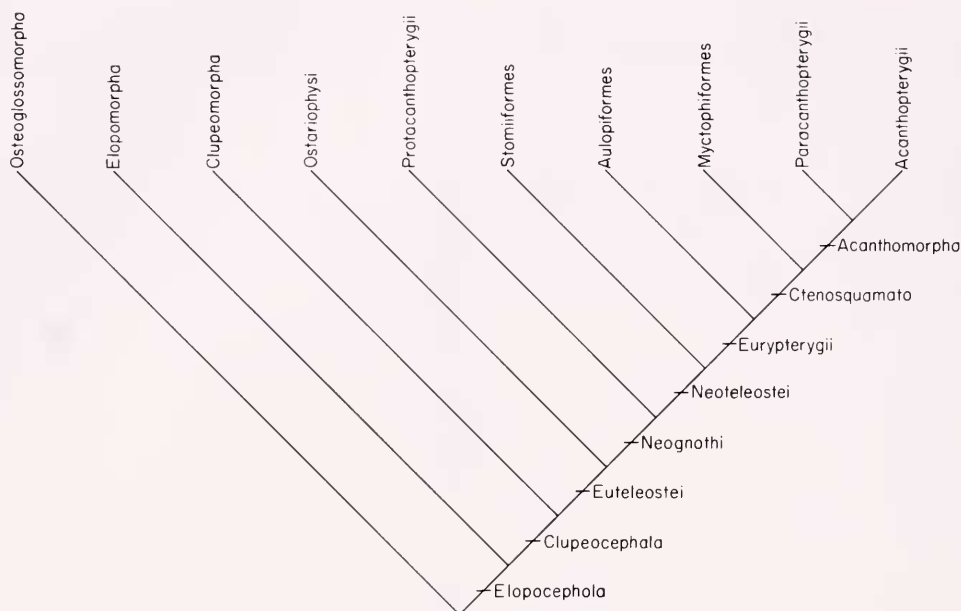


Figure 21. Recent concepts of phylogenetic relationships among the major teleostean lineages. Hypothesis of euteleostean relationships of Rosen (1973); non-euteleostean relationships hypothesized by Patterson and Rosen (1977).

organs include Jørgensen and Munk (1979), Hansen (1970), and O'Day (1973). Stomiiform photophores are non-bacterial (Herring and Morin, 1978; see also Baguet and Marechal, 1976).

According to Bassot (1970), stomiiform photophores can be described as follows: The walls of the photophores are formed of flat conjunctive cells filled with guanine platelets and covered laterally by a pigmented layer. This wall thus serves as a reflector. A gelatinous body appears to serve as a lens. The interior of the photophore consists of two cell types, A cells, the photocytes, which are densely packed and fill most of the photophore, and B cells, which Bassot describes as "glandular." Bassot notes that the properties of the photocytes are the same in all stomiiforms he examined. In primitive stomiiforms the photocytes are arranged roughly perpendicular to the center of the photophore, where there is a lumen (opening to the outside in the most primitive species); this is Bassot's Type Beta

photophore. In more specialized species, the lumen is not present and the photocytes are arranged either perpendicular to the center of the photocyte region (Type Gamma photophore) or are arranged in successive rows perpendicular to the main axis of the photophore (Type Alpha photophore). Weitzman (1974) noted that the distribution of the three photophore types corresponds well to his alignment of the sternoptychids, gonostomatids, and photichthyids and noted that, within the context of his proposed phylogeny, Bassot's Type Beta photophore is probably primitive for stomiiforms, while Types Alpha and Gamma are derived.

Some other teleosts have photophores, but none have photophores with morphology like those of stomiiforms. In the context of current hypotheses of teleostean phylogeny, photophores have evolved independently in numerous lineages. The following brief survey of non-bacterial photophores is based on the re-

view by Herring and Morin (1978) and is intended only to establish that, according to our knowledge of photophore morphology, the photophore structure of stomiiforms is unique. Much work remains to be done on photophore morphology in teleosts.

Among primitive teleosts, organized photophores are present in a single engrauid (*Coilia dussumieri*; Haneda, 1961) and in four alepocephalid genera, *Xenodermichthys*, *Photostylus*, *Rouleina*, and *Microphotolepis* (Herring and Morin, 1978). Best and Bone (1976) have described photophores of *Xenodermichthys* and *Photostylus* and found them to be unlike those of other teleosts (see their Fig. 2). A single species of *Rouleina* has small flat photophores in juvenile stages (Markle, 1978); these are apparently unlike those of stomiiforms.

Phylogenetically more advanced teleosts with photophores include the aulopiform scopelarchids *Benthallbalba infans* and *Scoperlarchoides kreffti*. Herring and Morin (1978) report that the photogenic tissue in these species is developed from ventral muscle tissues and that light is emitted through the ventral musculature. The evidence that photophores in these species are very different morphologically from those of stomiiforms, combined with lack of evidence that the two genera are more closely related to stomiiforms than to other scopelarchids, indicates that the photophores are independently derived.

Within the Myctophiformes, photophores are known in *Neoscopelus* species and in all myctophid genera and species; species in the two other neoscopelid genera, *Solivomer* and *Scopelengys*, lack photophores. According to Herring and Morin (1978), citing Brauer (1908) and Kuwabara (1954), photophores of *Neoscopelus* are different from those of myctophids. Examination of Brauer's Plate 31 shows that the photophores of *Neoscopelus* are different from those of stomiiform photophores. Myctophid photo-

phores are likewise distinct (see Fig. 9.11 of Herring and Morin, 1978) and different from those of stomiiforms, being relatively flattened and with less glandular tissue. Edwards and Herring (1977) have described photogenic tissues of myctophids as being composed of a number of flattened lamellae (see their Fig. 2).

Non-bacterial photophores are also reported to occur in the paracanthopterygian *Porichthys* and the perciform scaenid *Collichthys* (Herring and Morin, 1978); the phylogenetic remoteness of these genera from stomiiforms precludes further discussion.

Luminous tissues which are not organized into photophores have been reported in many teleostean groups, including stomiiforms. Structure of these tissues at the cellular level is unknown for the most part, and the systematic significance of their structure cannot be evaluated as yet.

2) Type 3 mode of tooth attachment. As defined by Fink (1981), Type 3 mode of tooth attachment has the following characteristics: The anterior mineralized border of the tooth is either close to the attachment bone at the tooth base and bound to it by collagen or ankylosed to the attachment bone. The posterior mineralized border is further from the attachment bone than the anterior border, leaving a larger portion of the posterior surface of the tooth collagenous; this flexible collagenous area is bound to the attachment bone. The tooth is hinged, or depressible, with its axis of rotation being the anterior tooth border.

Adult stomiiforms may have one or two of three modes of tooth attachment: Type 1 (fully ankylosed to the attachment bone), Type 3 (described above), or Type 4 (like Type 3 except the anterior mineralized border is free from the attachment bone and the axis of rotation is the collagenous tissue connecting the posterior tooth border with the attachment bone). Type 1 attachment mode is a primitive feature for teleosts (Fink, 1981).

Type 4 mode is found in juvenile stages of primitive stomiiforms, in the adults of some (perhaps paedomorphic) derived species (e.g., *Pollichthys*, *Vinciguerria*, *Valenciennellus*), and in many neoteleosts. Both Types 3 and 4 attachment modes are apparently the result of changes in the primitive teleostean pattern of tooth ontogeny.

Type 3 attachment mode occurs in adults of most stomiiforms, on either the jaws, the branchial apparatus, or both. On those bones where Type 3 is not found, either Types 1 or 4 are present; both of those modes are primitive for stomiiforms. Type 3 mode has not been found in any other group of teleosts.

3) Presence of a medial division of the adductor mandibulae muscle which is subdivided into two sections, a dorsal one inserting directly onto the maxilla, and a ventral one inserting onto the primordial ligament (Fig. 15A, B). Both the dorsal and ventral medial adductor sections were labelled $A_1\beta$ by Rosen (1973; Figs. 26 of *Astronesthes* and 23 of *Maurolicus*, respectively). Both these sections are present in *Diplophos*. Among many more specialized stomiiforms, one or the other of these is emphasized, and the other is reduced or lost. In a few members of the group, such as *Gonostoma* and *Margrethia*, additional sections are present. From our survey of adductor muscles within the stomiiforms, it appears that these muscles will be useful in analysis of phylogenetic relationships within the group.

Presence of a muscle inserting on the maxillary, either in the form of an A_1 (a dorsolateral division of the adductor mandibulae) or an $A_1\beta$ (a medial division of the adductor mandibulae) was deemed a neoteleostean character by Rosen (1973). We suggest, however, that these muscles are not homologous (at least in non-acanthopterygian teleosts) and that the mechanism of maxillary control cannot be synapomorphic for neoteleosts. The bases for our hypothesis are mor-

phology and the distribution of other characters (a parsimony consideration). The morphological evidence is that A_1 lies lateral to A_2 while $A_1\beta$ lies medial to A_2 . Thus, each muscle probably arises from different parts of the undifferentiated adductor during ontogeny. The distribution of other characters also supports our hypothesis. An A_1 is present in members of all the major eurypterygian lineages (aulopiforms, myctophiforms, paracanthopterygians, and acanthopterygians), indicating that it is a eurypterygian character. The distribution of $A_1\beta$, however, suggests that it has arisen as a neomorphic character several times: in stomiiforms, in myctophids, and at least once in acanthomorphs. In myctophids, for example, an $A_1\beta$ is present (Winterbottom, 1974, Fig. 4), while in the sister group of myctophids, the neoscolecids, there is an A_1 present but no $A_1\beta$ (Winterbottom, 1974, Fig. 3). In addition, in the sister group of the myctophiforms plus acanthomorphs, the aulopiforms, there is also an A_1 but no $A_1\beta$ (Rosen, 1973, Figs. 27–29). The simplest explanation of this distribution is that the common ancestor of the eurypterygians had an A_1 and that within the myctophoid lineage an $A_1\beta$ is an evolutionary novelty. Similar reasoning explains the presence of a medial adductor muscle in stomiiforms and acanthomorphs.

Because the muscles termed $A_1\beta$ in neoteleosts are hypothesized to be non-homologous, we refer to this muscle in stomiiforms simply as the medial division of the adductor mandibulae. For further discussion of adductor muscle morphology and nomenclature, see Winterbottom (1974). Lauder (1980) also comments on the medial adductor muscle in paracanthopterygians.

4) A premaxillary-rostrodermethmoid ligament extending from the dorsolateral aspect of the ethmoid to the contralateral premaxilla, or to both the contralateral and ipsilateral premaxillae (Fig. 12A, B). In some species, such as those of *Diplo-*

phos, the ligament from each side intersects and passes through that of the other side. Crossed dorsal ligaments are present in primitive members of the two major stomiiform lineages recognized by Weitzman (1974). Among these are *Neonethes*, *Photichthys*, and *Polymetme* (Weitzman, 1974, Fig. 49) of the Photichthya, and in the Gonostomata, *Gonostoma*, *Diplophos* (Fig. 12A, B), and as figured by Weitzman (1974), *Argyripnus* (Fig. 59, as premaxillary-proethmoid ligament), *Danaphos* (Fig. 57), *Maurolicus* (Fig. 55), and *Vinciguerria* (Fig. 50). In using this character as diagnostic of the Stomiiformes, we are accepting Weitzman's (1974) evidence regarding relationships of the major lineages; alternatively, should Weitzman's groups be found invalid, the premaxillary-rostrodermethmoid ligament could be used to propose a monophyletic group composed of the above-listed genera.

We have found no other teleosts with crossed dorsal premaxillary-rostrodermethmoid ligaments like those just described. In *Galaxias* there are two broad ligamentous sheaths extending from the dorsolateral aspects of the ethmoid to the posterodorsal and posterior surfaces of the ipsilateral and contralateral premaxillae. These sheaths are much broader than the ligaments of stomiiforms and, rather than extending primarily to the borders of the premaxillae, form a broad area of attachment on the posterior surfaces of the premaxillae.

In most teleosts there are no well organized ligaments between the rostrodermethmoid (or other dorsal ethmoid elements) and the premaxillae. But suspensory ligaments from the ethmoid region to the upper jaws are present in numerous teleosts, and the patterns of such ligaments may eventually prove useful in systematic analyses; nevertheless, pending a broad comparative study, we hesitate to make any further generalizations.

5) A single, broad proximal termination

of the second epibranchial which articulates with both the second and third pharyngobranchials. In other primitive teleosts the proximal termination of the epibranchial has two processes which form separate articulations with the pharyngobranchials. This character was noted by Rosen (1973: 441).

In *Diplophos* the articulation of the epibranchial with the second and third pharyngobranchials is extensive (see Figs. 10, 11). The epibranchial has a single proximal articular surface in all stomiiforms examined. Rosen (1973: 441) noted that epibranchial structure of some paralepidids is similar to that of stomiiforms; we agree with him that the similarity appears to be convergent.

6) Posterior branchiostegal abruptly larger (in a dorsoventral plane) than those more anterior. This morphology is present in most stomiiforms; in some derived species, the posterior two or three rays are abruptly larger than those more anterior (compare Fig. 9, herein, with Weitzman, 1974, Fig. 70 of *Argyripnus*).

In most other teleosts, the branchiostegals form a graded series, becoming progressively larger posteriorly. This is the case in, for example, *Hiodon*, *Elops*, *Etrumeus*, osmerids, galaxiids, salmonids, and myctophids; for a review and numerous figures of branchiostegal morphology, see McAllister (1968). An exception to the general teleostean condition is found in some acanthomorphs and a number of clupeomorph genera, in which the posterior three (or four) branchiostegals are abruptly larger than the two or three anterior (see McAllister, 1968, Pls. 9, 15, 19; Nelson, 1970, Figs. 7-9); this morphology is most parsimoniously interpreted as independently acquired in those acanthomorphs, clupeomorphs and in stomiiforms.

McAllister (1968: 48) suggested that "expansion of the upper one or two branchiostegals" characterize stomiiforms. He listed *Idiacanthus* as an exception; our specimens of that genus have the spe-

cialized branchiostegal. We do find, however, the posterior branchiostegal slender and unmodified in the malacosteid *Photostomias*, and we interpret this morphology as a secondary reduction.

7) Some branchiostegals articulating with the ventral hypohyals. This morphology is found in primitive and in most derived stomiiforms (Fig. 9). Exceptions, with branchiostegals restricted to the anterior and posterior ceratohyals, include the sternoptychids *Araiophos*, *Thorophos*, *Argyripnus*, *Sonoda*, *Polyipnus*, *Argyropelecus*, and *Sternoptyx* and the malacosteids *Aristostomias*, *Malacosteus*, and *Photostomias*. According to Weitzman's (1974) hypotheses of stomiiform and sternoptychid relationships, the lack of branchiostegals on the ventral hypohyals in these taxa is most parsimoniously interpreted as independently acquired in the *Thorophos-Araiophos* lineage, the lineage comprised of the other sternoptychid genera listed above, and in the malacosteids.

No other teleosts have been reported to have branchiostegals on the ventral hypohyals (McAllister, 1968), and we have found none.

8) Rete mirabilia and associated blood vessels located at the posterior of the swimbladder, except in those specialized species which lack the swimbladder. This morphology was suggested by Marshall (1960) to be unique to "stomiatoids." In contrast, most other teleosts with retia have them anterior to or near the middle of the gasbladder, with the vascular system extending from anterior to the rete; compare gasbladder morphologies illustrated in Marshall (1960: Figs. 30, 36). In some protacanthopterygians no organized rete is present; in some mid-water oceanic protacanthopterygians, such as *Opisthoproctus*, numerous "micro-retia" are present (Marshall, 1960, Fig. 4D). Fänge (1953) illustrated swimbladder morphology and rete distributions in several phylogenetically advanced teleosts.

The only other teleosts noted by Marshall as having a posteriorly positioned rete are the berycoids *Stephanoberyx*, *Anoplogaster*, and *Melamphaes*. In these, however, the structure of the rete is more specialized and there is an oval window. In addition, other characters (see Rosen, 1973) indicate that these genera cannot be seriously considered as the sister group of stomiiforms.

The value of swimbladder morphology for diagnosing stomiiform monophyly needs to be further tested by broad comparative studies.

The characters presented above should serve to diagnose the Stomiiformes. Other authors have suggested other characters, but we have not been able to corroborate their value in our analysis. Regan's (1923) characterization of the group is inadequate because the characters either are not adequately described or are applicable at a more general level of analysis. More recently, Greenwood *et al.* (1966) considered a number of characters to be diagnostic of the "stomiatoids," including "photophores, a large basisphenoid associated with the absence of lateral prootic walls in the anterior region of the posterior myodome" (the "post-basisphenoid space" of Weitzman, 1967a), "preopercular and infraorbital lateral-line canals connected by the supraorbital canal in the frontal, often a dorsal and in some cases a ventral adipose fin, and a mesocoracoid in those members with well developed pectoral fins" (p. 372). We have discussed photophore morphology above. The "post-basisphenoid space" is present as described only in some of the more phylogenetically derived species (e.g., melanostomiids, *Astronesthes*; see Fig. 5 of Greenwood, *et al.*, 1966 and compare with Fig. 4, herein). We were unable to find lateral-line canals as described in specimens we examined of numerous stomiiform genera. A dorsal adipose fin is a cuteleostean character (Patterson and Rosen, 1977), and a ventral adipose fin is

present in only some, phylogenetically derived species, e.g., *Stomias*, *Chauliodus*. A mesocoracoid and a large basisphenoid are primitive for teleosts.

MONOPHYLY AND INTERRELATIONSHIPS OF THE NEOTELEOSTEI

The most recent discussion of the Neoteleostei is that of Rosen (1973) (Fig. 21). He diagnosed the group on the basis of three characters (p. 505): 1) presence of a retractor arcuum branchialium muscle, RAB (called retractor dorsalis, herein); 2) presence of ascending and articular premaxillary processes (he listed this character in stomiiforms as occurring "in some members of the gonostomatid-stenopterygoid complex"); and 3) presence of "an advanced type of internal maxillary muscle ($A_1\beta$)."

Rosen included stomiiforms in the Subdivision Neoteleostei since they appeared to share these characters with other neoteleosts. On the basis of a number of characters, stomiiforms were considered to be the sister group (Stenopterygii) of all other Neoteleosts (Eurypterygii). The Eurypterygii was diagnosed on the basis of eight characters (these are discussed below).

Stomiiforms have in recent decades been considered related to either clupeoids or salmonoids (see Weitzman, 1967a). Greenwood *et al.* (1966) placed them within the Salmoniformes and, with the exception of Rosen's (1973) paper, this arrangement has remained the accepted one by general consensus (see Nelson, 1976; textbooks by Bond, 1979, and Lagler *et al.*, 1977).

Our own analysis of Rosen's characters and others indicates that Rosen's basic conclusions are corroborated, i.e., that stomiiforms are neoteleosts and that they are the sister group of the monophyletic Eurypterygii. We present further evidence for neoteleostean monophyly immediately below and then discuss Ro-

sen's (1973) work on the Neoteleostei and Eurypterygii. In the next section, on protacanthopterygian relationships, we discuss our findings regarding previous hypotheses about the Salmoniformes.

Characters shared as synapomorphies by neoteleosts include the following:

1. A retractor dorsalis muscle is present. It is lacking in most non-neoteleosts (Rosen, 1973; see Winterbottom, 1974, regarding the distribution and nomenclature of this muscle and a similar one in cyprinids, gars, and *Ambloplites*). We have confirmed the presence of the retractor dorsalis in *Diplophos*.

2. A rostral cartilage is present. The cartilage is a single median structure which lies between the premaxillae and the ethmoid region of the neurocranium. We have seen this cartilage in all major neoteleostean lineages examined, and it is illustrated several times by Rosen and Patterson (1969; see for example Figs. 15C, *Typhlichthys*; Fig. 74B, *Chlorophthalmus*; Fig. 74C, *Neoscopelus*; Fig. 74E, *Myctophum*). A rostral cartilage is lacking in many phylogenetically derived stomiiforms (e.g., melanostomiids) and in paralepidids.

Paired cartilage bodies lie anterolateral to the ethmoid region, usually between the palatine, maxilla, and ethmoid, in a number of primitive teleosts. In salmonids, paired cartilages lie along or just lateral to the midline, between the ethmoid and the premaxillae. Fusion of these cartilages would result in a body identical in form to a rostral cartilage, and it is possible that such was its origin. This possibility is considered in more detail in the discussion of protacanthopterygian interrelationships.

3. Teeth with attachment mode Type 4 (Fink, 1981). Non-neoteleosts have the primitive modes 1 and 2, with one exception noted below (see discussion of stomiiform monophyly, above, for definitions of attachment modes). Teeth with Type 4 attachment mode are hinged, with the anterior border of the tooth base

free from the underlying attachment bone, and with a relatively large unmineralized collagen area at the posterior border of the tooth base. The axis of rotation is the posterior collagen area. As discussed above in the section on stomiiform characters, and by Fink (1981), Type 4 teeth are found in juveniles of several primitive stomiiform species (including *Diplophos* and *Photichthys*), in several species with small adults, including *Pollichthys*, *Vinciguerria*, and *Valenciennellus*, and in the larger melanostomiatiid *Tactostoma*. Fink (1981) found that when hinged teeth are present in aulopiforms, myctophiforms, paracanthopterygians, beryciforms, and perciforms, they have Type 4 mode of attachment.

In most adult stomiiforms, the hinged teeth are of Type 3, but the presence of Type 4 mode in juveniles of primitive stomiiforms and in adults of some other species (usually in which individuals are small) suggests that Type 4 teeth were present in the common ancestor of all neoteleosts and that the character is thus a neoteleostean synapomorphy.

The only other teleost in which Fink (1981) found Type 4 attachment mode was *Esox*. He concluded that details of morphology, combined with a lack of evidence linking *Esox* with neoteleosts, indicates that the Type 4 mode of *Esox* is independently derived.

4. The exoccipital and basioccipital bones both articulate with the vertebral column (anterior centrum and/or notochord) (Figs. 5, 7). In other teleosts examined, with two exceptions discussed below, only the basioccipital articulates with the vertebral column. The neurocranium/vertebral articulation in *Diplophos* is similar to that of other primitive stomiiforms such as *Photichthys* and *Polymetme* (the figure of the latter in Weitzman, 1967a, Fig. 13, is not accurate in that the exoccipitals should extend more posteriorly). The neurocranium/vertebral articulation is illustrated for the sternopychid genera in Weitzman (1974). In

more specialized stomiiforms, the posterior process of the exoccipital is enlarged, sometimes greatly (see Weitzman, 1967b, Figs. 5, 6, 13 for *Astronesthes*), and articulates with the thick connective tissue sheath overlying the notochord. The inclusion of both the exoccipital and basioccipital bones in the vertebral articulation was illustrated by Rosen and Patterson (1969) for aulopiforms (Figs. 61B, 63), neoscopecelids (Figs. 61A, C; 63), myctophids (Fig. 61D), paracanthopterygians (Fig. 10A–D, among others), and acanthopterygians (Fig. 10E). Our own observations confirm the distribution of this character. Weitzman (1974: 360–361) has described the condition of the articulation in osmerids and stomiiforms in greater detail.

Among non-neoteleosts we find the exoccipital included in the neurocranium/vertebral articulation in the osteoglossomorph *Hiodon* and in salmonids. In *Hiodon* the anterior vertebral centrum is firmly and closely articulated with the neurocranium; the anterior face of the centrum is convex and fits into a concavity formed by the basioccipital and exoccipital. In other osteoglossomorphs examined (*Osteoglossum*, *Arapaima*, *Scleropages*) and in notopterids (Greenwood, 1963), the articulation includes the basioccipital only. We surmise, in the context of the well documented hypothesis that osteoglossomorphs are the sister group of elopocephalans (Patterson and Rosen, 1977), that the morphology in *Hiodon* is an independent acquisition and that it may be in part related to the expansion of the exoccipitals as a part of the otophysic connection in those fishes (see Greenwood, 1973, Pl. 1).

In salmonids, the neurocranial articulation is virtually the same as that of neoteleosts, with the basioccipital and exoccipitals articulating with the anterior vertebra, and it may be that the two are sister groups. This possibility is discussed in more detail below in the section on interrelationships of protacan-

thopterygians. Should the hypothesis of this relationship be corroborated with further investigation, this character would apply to an expanded Neoteleostei (including salmonids) or to a taxon with a new name.

Two of the three character complexes used by Rosen (1973) to define the Neoteleostei appear to be invalid. These are presence of an $A_1\beta$ division of the adductor mandibulae muscle and upper jaw structure. Our opinions regarding homologies of the adductor muscles are given in the preceding section on stomiiform monophyly; we believe that the adductor muscle morphology of stomiiforms is unique to them.

Regarding upper jaw morphology, the situation is more complex. In his diagnosis of the Neoteleostei, Rosen lists presence of both ascending and articular premaxillary processes (1973: 505). However, in the text (p. 413), he also includes some other upper jaw features shared by "... more generalized gonostomatid and sternoptychid stomiatoids ..." as neoteleostean features, including "... a low post-maxillary process on the premaxilla; a somewhat folded head on the maxilla; various ligaments extending between the palatine and ethmoid; and both upper jaw bones, in some cases, in a neoteleostean pattern (Weitzman, in press)." Some of these are easily dismissed. Weitzman (1974, cited as in press by Rosen) discussed and illustrated jaw bones in certain stomiiforms, but not those of other neoteleosts, and, as far as we know, a neoteleostean jaw bone pattern has not been defined. Presence of "various ligaments extending between the palatine and ethmoid," not defined further, is so ambiguous as to be meaningless; in fact the presence of some ligaments between the palatine and ethmoid appears to be primitive for teleosts. We find no neoteleostean palatine-ethmoid ligament pattern.

We have found articular processes (a dorsal projection of bone articulated with

the maxillary head) to be common among elopocephalans, and therefore primitive for neoteleosts. No ascending process (i.e., a dorsal projection of bone medial to the articular process) has been found by us in stomiiforms. Rosen (1973) apparently interpreted the articular process in *Maurolicus* and *Neophos* (= *Thorophos* in Weitzman, 1974) as an ascending process; nevertheless, it is clear that the process in each of these examples is closely articulated with the maxilla (see Weitzman, 1974, Fig. 55 of *Maurolicus* and Fig. 51 of *Thorophos*).

We are not certain about what Rosen means when he refers to the "folded head of the maxilla." He may be referring to the morphology found in some eurypterygians wherein the proximal end of the maxilla extends dorsally over the premaxilla, or in which the maxilla is bifurcated anteriorly and extends around the ascending or articular process of the premaxilla (see, for example, Rosen and Patterson, 1969, Fig. 15 of percopsiforms). Although some stomiiforms may have an anteromedial groove in the maxilla, we have not found what we would consider a "folded head" in any stomiiform we have examined.

A post-maxillary process on the premaxilla was also considered by Rosen to be a neoteleostean synapomorphy. However, we find that such a process is absent in primitive stomiiforms, such as *Diplophos* (Fig. 4), *Polymetme* (Weitzman, 1967a, Figs. 13, 14), *Thorophos* (Weitzman, 1974, Fig. 18), and *Gonostoma*. A small bony flange extends dorsally from the premaxilla, medial to the maxilla, in *Maurolicus* (Weitzman, 1974, Fig. 22). An elongate flange also projects medial to the maxilla in *Valenciennellus* (Weitzman, 1974, Fig. 25). These latter two genera are in the Sternoptychidae, a group considered by Weitzman (1974) to be phylogenetically derived relative to the lineages represented by *Diplophos*, *Polymetme*, and *Gonostoma*. This indicates that the processes in *Maurolicus* and

Valenciennellus are specializations of those genera.

Rosen (1973) considered stomiiforms to be the sister group of other neoteleosts, the Eurypterygii (Fig. 21). The latter was considered monophyletic on the basis of eight characters (Rosen, 1973: 505–506). One character, presence of a protractor pectoralis muscle, has been found by Greenwood and Lauder (1981) to be a gnathostome synapomorphy. Two other characters should be reassessed since they both are described as “tendencies”; these are a tendency for the alveolar arm of the premaxillary to elongate and develop a post-maxillary process, and a tendency for the pectoral fins to “migrate up” on the flank and for the pelvics to move forward under the pectorals (see Introduction for discussion of evolutionary “tendencies” as characters). A fourth character, “stabilization of the ascending and articular premaxillary processes” must be assessed in view of our finding that stomiiforms have an articular process but not an ascending process. This would imply that presence of the latter character is a eurypterygian trait (see also Rosen and Patterson, 1969). Another character listed by Rosen is “development of a deeply folded articular head on the maxilla” as opposed to a “somewhat folded head on the maxilla” in stomiiforms (Rosen, 1973: 413). As noted above, eurypterygians do have a specialized maxillary morphology and this may also be a eurypterygian character; more precise descriptions are needed for further analysis.

A sixth character, an “elongate third pharyngobranchial that displaces the second pharyngobranchial from the midline . . .,” appears to diagnose two groups, the Eurypterygii and a subgroup of the Stomiiformes (Fink, in preparation). The few instances of eurypterygians with the second pharyngobranchial not displaced by the third occur in a pattern which is incongruent with current concepts of relationships within the group, so it is most

parsimonious to assume that they have developed the pattern as a neomorphic feature (e.g., *Hoplostethus*, Rosen, 1973, Fig. 88).

The seventh character considered by Rosen (1973) to be a eurypterygian synapomorphy is “reduction of the second preural neural spine in the caudal skeleton to a half-spine, and the forward migration of the epurals.” “Reduction” in neural spine morphology is also present in many primitive euteleosts, including esocoids (see discussion by Rosen, 1974: 292), some salmonids (e.g., *Prosopium* and *Coregonus*), and some osmerids. Whether this character is eurypterygian or applicable to a broader level of relationships is problematical, depending on assessment of relationships among the primitive euteleostean groups. At this point, however, the character does seem to diagnose the Eurypterygii. As noted by Rosen and Patterson (1969) the evolution of neural spine morphology has been complex; descriptions which clearly differentiate the various “reductive” spine morphologies for systematic purposes are not yet available. Regarding the “forward migration of the epurals” (Rosen, 1973: 506), we find no distinction between the placement of epurals in primitive eurypterygians and non-eurypterygians (compare Weitzman, 1967a, Fig. 4 of *Spirinchus*, and Rosen and Patterson, 1969, Fig. 2B of *Aulopus* with *Diplophos*, our Fig. 16).

The remaining character suggested by Rosen (1973) as diagnostic of the Eurypterygii is “a large tooth plate fused with the underside of the third epibranchial.” Fusion of a toothplate to the third epibranchial is a feature which we have found only in eurypterygians and which does diagnose the group (the toothplate is lacking in ateleopodids, Rosen, 1973: 487). We would suggest that reference to tooth plate size can be eliminated, however, since in some perciforms, such as *Perca*, the tooth plate is small.

From our discussion above concerning

characters considered to be neoteleostean by Rosen, it would appear that some of them may be eurypterygian. These would include the presence of an ascending premaxillary process, a "folded head on the maxilla," and a post-maxillary process on the premaxilla. Further examination of the distributions of these characters is needed for a better assessment of them.

Lauder (1981) presents another eurypterygian character: presence of an interoperculo-hyoid ligament.

In summary, we agree with Rosen's (1973) hypotheses that the Neoteleostei and Eurypterygii are monophyletic and that the latter is the sister group of the Stomiiformes.

COMMENTS ON PROTACANTHOPTERYGIAN INTERRELATIONSHIPS

The traditional inclusion of stomiiforms in "basal" teleostean groups led us to examine a number of members of the various phylogenetically primitive euteleostean lineages. As noted by Rosen (1974), the Protacanthopterygii of Greenwood *et al.* (1966) has undergone steady attrition as the included groups have been placed into a more phylogenetic framework. The most recent treatment of the Protacanthopterygii (now including only the Salmoniformes) is that of Rosen (1974). We have examined the arguments for his classification within the group and present herein some discussion of his hypotheses of relationships. Rosen's (1974) contribution is examined in detail since its methodology is explicitly phylogenetic, and thus its hypotheses are ideally constructed for criticism. We make few comments on the work of other authors (e.g., Greenwood *et al.*, 1966; Weitzman, 1967a; McDowall, 1969; Gosline, 1960; Klyukanov, 1975), since none of them used explicitly phylogenetic methodology, and thus their concepts of relationship and character usage cannot be inter-

preted unambiguously. It is not our purpose here to provide a revision of the protacanthopterygians, but rather to present the findings that have emerged from our survey of lower teleosts, pending a more thorough survey of relationships at this level.

Rosen (1974) summarized his hypotheses concerning protacanthopterygian relationships in two places, first on page 310 and then in an "analytical" key (pp. 311–313). His hypothesis of protacanthopterygian relationships can be summarized as follows (Fig. 22). There are two major lineages. One, Infraorder Esocae, includes the Esocidae, Umbridae, and Lepidogalaxiidae; the other, Infraorder Salmonae, includes two suborders, the Argentinoidei and Salmonoidei. The Argentinoidei is comprised of the Argentinoidea and the Alepocephaloidea, and the Salmonoidei is comprised of the Salmonoidea (Salmonidae and Galaxiidae) and the Osmeroidea (Osmeridae, Plecoglossidae, Retropinnidae, and Salangidae). When formal group names are mentioned in the text below, they will correspond to Rosen's usage. When our conclusions differ from his, our use of his categories as descriptive terms follows these conventions: presumed polyphyletic groups (e.g., "salmonoids") are used with quotes, and paraphyletic groups (e.g., osmeroids) are used without quotes. The term argentinoidei as used below refers to the subordinate Argentinoidei, not to the superfamily Argentinoidea. Esocoid refers to members of both the Infraorder Esocae and the Esocoidei, since they are redundant categories in the classification (though only provisionally accepted herein).

Rosen's (1974: 311–314) "analytical key" is ambiguous about which characters were used as synapomorphies for which groups. For most of the characters both the derived and primitive states are given in a single couplet; thus the derived state is synapomorphic at some lower taxonomic level and not diagnostic

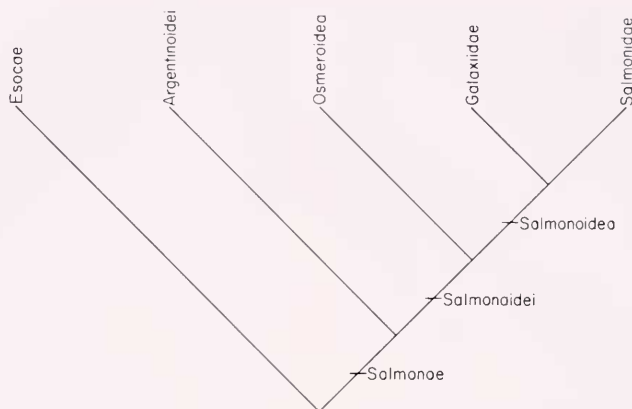


Figure 22. Rosen's (1974) hypothesis of choice for protacanthopterygian relationships.

of the group that "keys out" at that couplet. In some cases, characters were used as synapomorphies at several levels in the key, without explanation. In spite of the confusing structure of the key, a careful reading of it, combined with a reading of the text, does provide some characters which appear to be diagnostic of the various groups recognized by Rosen.

Our discussion of Rosen's hypotheses follows the sequence of taxa as given in his key, which the reader may wish to consult.

The Protacanthopterygii was never explicitly diagnosed by Rosen, but the characters which he suggested to unite esocoids (including *Lepidogalaxias*) with the other lineages can be construed as protacanthopterygian synapomorphies. These characters were discussed on page 310 and include fusion of a toothplate (when present) to the third pharyngobranchial and presence of "a posterior toothplate below the fourth pharyngobranchial and fourth epibranchial in a pattern like that of the 'well toothed' salmoniforms." However, the first of these characters is probably clupeocephalan, since fusion of the toothplate occurs not only in salmoniforms but also in *Etrumeus*, ostariophysans, stomiiforms, and almost all eurypterygians (with the ex-

ception of the Ateleopodidae, noted by Rosen, 1973: 487). Concerning the second character, Rosen did not precisely define the pharyngobranchial toothplate "pattern" or "well toothed," but we assume that he is referring to the presence of but a single toothplate associated with the fourth pharyngobranchial and fourth epibranchial. This character has a distribution in the Protacanthopterygii which indicates that convergence is common. There are two toothplates in this position in argentinoids we examined, in galaxiids (see Rosen, 1974, Fig. 11b, c), and in some osmeroids (see Rosen, 1974, Fig. 12b). It would appear that the fusion (or loss) of the toothplate on the fourth pharyngobranchial has occurred in salmonids, some osmeroids, and esocoids, and that the character cannot be definitive for the Protacanthopterygii. Rosen admits that the evidence for inclusion of esocoids in the group is "slight," and we agree.

Of the eleven characters Rosen (1974) used to place *Lepidogalaxias* in the Esocae, only four appear to be appropriate for inference of relationship between those groups: lack of a mesocoracoid, lack of pyloric caeca, a single rudimentary neural arch and spine over PU1, and a single uroneural. In view of the reductive

nature of all of these characters and the very small size and benthic "habits" of *Lepidogalaxias*, and in view of the importance of the biogeographic hypothesis suggested by this hypothesis of relationships, it appears to us that a further search for characters is warranted. This is especially so since in the original description of *Lepidogalaxias*, Mees (1961: 33) states that there is a single series of comparatively large teeth on the entopterygoids (mesopterygoids, herein), a character which we propose below to be a synapomorphy for osmeroids (including galaxiids); Rosen (1974) states that *Lepidogalaxias* lacks teeth on the bone. This contradictory evidence needs to be reexamined.

Of the thirteen characters listed in Rosen's key as diagnostic of the Infraorder Salmonae, only one appears to represent a possible synapomorphy: lack of a toothplate on the fourth endoskeletal basi-branchial. Rosen's text (1974: 237) would appear to contradict the utility of this character, since he reports the toothplate in *Retropinna* and *Osmerus*, both members of the Salmonae. While we have not found the toothplate in specimens of those genera available to us, we nevertheless doubt the utility of the character as diagnostic of the Salmonae since the toothplate is also lacking in other primitive euteleosts, including ostariophysans (except the phylogenetically derived characiform *Prochilodus* and, according to Rosen, the characiform *Ichthyborus* [1974: 273]), stomiiforms and aulopi-forms. Dentigerous toothplates are present on the fourth basibranchial of *Elops*, *Megalops*, *Hiodon*, and *Chirocentrus* (but lacking in all other clupeomorphs). This distribution pattern suggests to us that the Esocae, whose members have the toothplate, may be the sister group to all other euteleosts (the toothplate is also reported in *Lepidogalaxias* by Rosen, 1974).

Two additional characters of the Salmonae are listed in Rosen's text (p. 310):

presence of fanglike teeth arranged marginally on the basihyal and development of platelike bone on the posterior neural and hemal spines. Interpretations of the term "fanglike" will vary with each investigator, and we find a morphological continuum from "large fanglike" to "small fanglike" to "teeth along the lateral basihyal border somewhat larger than those on the medial surface of the bone." These definitions are of necessity highly subjective and are best understood by an examination of actual specimens. Large, fanglike, and usually recurved teeth, proportionally much larger than teeth found in other primitive euteleosts, are found in salmonins (e.g., *Cristivomer*, *Salvelinus*, *Salmo*, *Onchorhynchus* [Rosen, 1974, Fig. 3A-E, respectively], and *Brachymystax*), and in the osmerid *Spirinchus*. In *Osmerus* large "fanglike" teeth are present around the anterior region of the basihyal, but the more posterior teeth are all much smaller, and those along the border are about equal in size to those on the medial portion of the bone. Teeth which are "fanglike" and recurved but not large are found in galaxiids, *Retropinna*, and *Argentina*. Genera in which the marginal basihyal teeth are somewhat larger than those on the rest of the bone include the osmerids *Hypomesus* and *Mallotus* (Rosen, 1974, Fig. 2A, B) and our specimens of *Plecoglossus*; Rosen's figure of *Plecoglossus* (2C) shows a scattering of larger teeth among some smaller teeth. We found that basihyal teeth in *Prosopium* (Rosen, 1974, Fig. 3F) and *Thymallus* to be uniformly small. Basihyal teeth are either small in both size and number or not present in most argentinoids (Greenwood and Rosen, 1971).

This cursory and incomplete survey of basihyal tooth morphology indicates to us that presence of enlarged marginal basihyal teeth would be diagnostic of the Salmonae, if the presence of small teeth in some salmonids and argentinoids is found to be a secondary reductive fea-

ture. This can only be assessed in the context both of more characters and of hypotheses of phylogenetic relationships within the various protacanthopterygian groups.

Platelike bone on the neural and hemal spines, the second character of the Salmonae listed in Rosen's text, is well developed in many members of the group (see Rosen, 1974, Figs. 18, 19, 25–27; Gosline, 1960). We find use of this character difficult because of our uncertainty about what Rosen intended by "plate-like." In many members of the Salmonae there is extensive laminar bone on the neural and hemal spines, forming large blade-like structures (see Rosen, 1974, Figs. 18A, *Galaxias vulgaris*; 25B, *Salmo*; 26C, *Plecoglossus*; 27D, *Retropinna*). In other members of the group, the lamellar bone is less extensive, often forming ovoid anterior extensions from the spines (see Greenwood and Rosen, 1971, Figs. 11B, *Searsia*; 12B, *Glossanodon*; 14, *Bathylagus*; 16A, *Osmerus*). In yet others, there is very little or no lamellar bone on the spines (see Greenwood and Rosen, 1971, Figs. 8, *Talismania*; 10, *Rouleina*; Rosen, 1974, Fig. 19, *Aplocheilichthys*; Weitzman, 1967a, Fig. 4, *Spirinchus*). In *Cristivomer*, the neural spines have little lamellar bone, while on the hemal spines it is more extensive. In primitive teleosts generally, some lamellar bone on the neural and hemal spines in the caudal region is common, e.g., in *Elops*, *Denticeps*, many characiforms, and *Aulopus* (it is extensive and blade-like in the latter). Nevertheless, it could be argued that some amount of elaboration of lamellar bone is a diagnostic character of the Salmonae and that its absence in some members of the group (e.g., alepocephaloids, *Spirinchus*) is a secondary loss. We would like to see a more precise definition of the character, however, than that provided by Rosen (1974).

Rosen (1974) diagnosed the suborder Argentinioidei on the basis of three unique characters: basibranchial tooth-

plate with a sharp ridge of bone and a membrane that divides the orobranchial chamber into right and left halves, presence of a cruminal organ, and accessory cartilage at the posterior end of the fifth ceratobranchial; see also Greenwood and Rosen (1971).

The suborder Salmonoidei is undefined by the characters presented by Rosen (1974).

The superfamily Salmonoidea (Salmonidae and Galaxiidae, including Aplocheilichthinae) is diagnosed by Rosen by the presence of paired marginal basihyal teeth, none or few scattered teeth on the basibranchials, and the fourth epibranchial without uncinate or levator processes. Paired basihyal teeth, rather than alternating teeth with a single tooth at the anterior apex of the bone, are found in most salmonids and many specimens of galaxiids. However, about half of the galaxiids we examined have a single terminal tooth and alternating tooth pairs along the basihyal margin. In addition, some osmeroids approach the "paired" tooth condition (see, e.g., Fig. 4A, C of Rosen, 1974). Lack of teeth or presence of a few scattered teeth on the basibranchials is a character present also in argentinoids and stomiiforms. Lack of an uncinate process on the fourth epibranchial is not a feature common to all galaxiids; our specimens of both *Galaxias anomalous* and *G. delfini* have such a process. Loss of the uncinate process appears therefore to be independent in salmonids and galaxiids. Absence of a "levator process" is a character which, as defined, may lead to confusion. In teleosts generally a levator muscle attaches to the dorsolateral surface of the fourth epibranchial (Winterbottom, 1974). In many primitive euteleosts, this surface is separated from the ventrolateral extremity of the bone by a concavity, so that the area of levator insertion may be termed a process. Rosen's character, "absence of a levator process," might better be defined as loss of this concavity; the area of levator attachment

remains unchanged, although in descriptive terms it is no longer a process. Absence of this concavity is a feature shared not only by salmonids and galaxiids, but also by the osmeroids *Stokelia*, *Retropinna*, *Salangichthys*, and by esocoids, except *Umbra*.

Thus, of the four features suggested by Rosen to be synapomorphies for his Salmonoidea, two (paired basihyal teeth and no uncinat process) are not always present in galaxiids, one (reduced basibranchial dentition) is shared also with argentinoids (and stomiiforms), and the other (no distal concavity in the epibranchial) is shared with esocoids and some osmeroids. We would prefer a search for other characters to substantiate monophyly of the Salmonoidea, particularly since we have found evidence, presented below, which suggests other relationships for both the galaxiids and the salmonids.

The Osmeroidea (including Salangidae, Osmeridae, Plecoglossidae and Retropinnidae), is diagnosed in Rosen's key by two characters which appear to represent possible synapomorphies. These are the presence of a blunt, somewhat elevated median ridge on the second basibranchial toothplate, except when the toothplate is greatly expanded, and lack of autogenous rudimentary neural arches dorsal to PU1, these arches having become fused into a dorsal outgrowth of the first uroneural. In the osmeroids examined by us (*Osmerus*, *Mallotus*, *Spirinchus*, *Hypomesus*, *Retropinna*), the basibranchial toothplate is smoothly, though fairly steeply, arched dorsally along most or all of its length. No blunt median ridge is present. The basibranchial toothplate is similarly shaped in *Elops*, *Megalops*, *Chirocentrus*, *Aulopus*, and *Neoscopeplus*, and would appear therefore to be primitive in form in osmeroids. The second osmeroid character of Rosen (1974: 313) is the presence of a "stegural," defined as a complex formed by fusion of the rudimentary neural arch(es) of PU1

to the first uroneural (see also Greenwood and Rosen, 1971). Rosen contrasted this condition with that of salmonids, wherein the rudimentary neural arches "join" but do not fuse with the uroneural, forming a "primitive stegural" (Patterson and Rosen, 1977: 122–126, have recently redefined the term stegural, so we enclose the "stegural" of Rosen, 1974, in quotation marks). Our observations confirm that adult osmeroids do have the rudimentary neural arches fused to the first uroneural, and that this appears to be part of an ontogenetic sequence, since in our smaller specimens the arches are not yet fully fused with the uroneural (see Rosen, 1974, Fig. 28). We have observed the bones to be fused in adults of *Retropinna*, *Mallotus*, *Spirinchus*, *Hypomesus*, and *Osmerus*. Some osmeroids also have the rudimentary neural arches fused with PU1, but such fusion apparently occurs later in ontogeny than fusion to the uroneural; a large (154 mm SL) specimen of *Osmerus* (MCZ 56535) has two large rudimentary neural arches over PU1 and fused with both the uroneural and the centrum. Fusion of rudimentary neural arches to both the uroneural and PU1 are found in some argentinoids and galaxiids also, but in these fishes fusion to the uroneural appears to occur later in ontogeny than fusion to PU1. Most of the galaxiids examined by us are small specimens and have the arch(es) fused with the centrum but not the uroneural; however, in a 238 mm SL specimen of *Galaxias delfini* (MCZ 46284) there are two rudimentary neural arches fully fused with both the centrum and the uroneural. Two small specimens (44 mm and 71 mm SL) from the same collection as that specimen have the arches unfused with the uroneural. Rosen noted fusion of the neural arches to the uroneural in some galaxiid specimens (1974: 296, Figs. 18E of *Galaxias maculatus*, 19B of *Aplocheilichthys tae-niatus*, 19C of *Lovettia seali*), but he did not indicate sizes of the specimens he examined.

To summarize our observations on rudimentary neural arch/uroneural fusion patterns, there appear to be two fusion patterns of these bones in protacanthopterygians. In argentinoids and galaxiids, when fusion takes place, the arches fuse first with the centrum and then with the uroneural. In osmeroids, the arches fuse first with the uroneural and then, in some cases, with the centrum. Salmonids, many argentinoids, and esocoids do not have uroneural/rudimentary neural arch fusion. The phylogenetic significance of the two fusion patterns is unclear at present, and a decision as to whether they suggest that argentinoids and galaxiids are sister groups and that osmeroids are monophyletic, or whether the fusion pattern of either of these two "groups" is primitive, must await more detailed analysis and comparisons in the context of other characters.

In addition to the various protacanthopterygian characters listed above, fusion of the fifth epibranchial to the fourth was discussed in detail by Rosen (1974: 284, Figs. 8–10, 14, 16). He considered fusion between the dorsal tip of the fifth epibranchial and the midpoint of the dorsolateral border of the fourth epibranchial to be an additional derived character for the Salmonioidea (Salmonidae plus Galaxiidae). Similarly, a fusion of the ventral tip of the fifth epibranchial to the posteroventral end of the fourth was considered derived for the Osmeroidea. However, Rosen found fused epibranchials only in one salmonid, *Prosopium*, and in some osmeroids there was no fusion. Use of these fusions as characters at the "salmonoid" and osmeroid levels presumes loss of fusion in some members of each group. Such a presumption appears unwarranted at this time, since the current lack of information on both osmeroid and salmonid phylogeny precludes a parsimony assessment.

As should be evident from our survey of the most recent presentation of evidence regarding protacanthopterygian

relationships, we think that alternative hypotheses should be considered. A full analysis of protacanthopterygian interrelationships is beyond the scope of this paper, but we interpret below some morphological evidence examined during the course of this study; our hypotheses of relationship are illustrated in Figure 23.

Several features were found which might be synapomorphous for a group consisting of osmeroids and galaxiids (*sensu* Rosen, 1974) and thus supportive of previous workers' conjectures (Gosline, 1960; McDowall, 1969). First, in members of both groups there is a series of large teeth along the medial border of the mesopterygoid (in some osmeroids, such as *Retropinna* and *Plecoglossus*, there are also some smaller teeth lateral to the large serial teeth). In most primitive teleosts with mesopterygoid teeth, including *Elops*, *Megalops*, *Etrumeus*, and *Diplophos*, the teeth are small and scattered over the ventral surface of the bone. Large, serially arranged mesopterygoid teeth are present in *Scleropages* and *Osteoglossum*, but the evidence that these osteoglossomorphs are phylogenetically distant from osmeroids is quite strong (Patterson and Rosen, 1977) and the similarity is considered by us to be convergent.

We suggest that in osmeroids and galaxiids there is a specialized "tongue bite" mechanism in which food is manipulated between the basihyal teeth and the mesopterygoid teeth. This would parallel the "tongue bite" in the osteoglossomorphs mentioned above. In some salmonids, including *Salmo* and *Oncorhynchus*, there is also a morphology which appears to be a "tongue bite" mechanism, but in these fishes the dorsal teeth lie on the greatly elongated vomer and the mesopterygoid is toothless (as in all salmonids).

A second feature shared by osmeroids and galaxiids is the lack of a basisphenoid bone, apparently a derived condition.

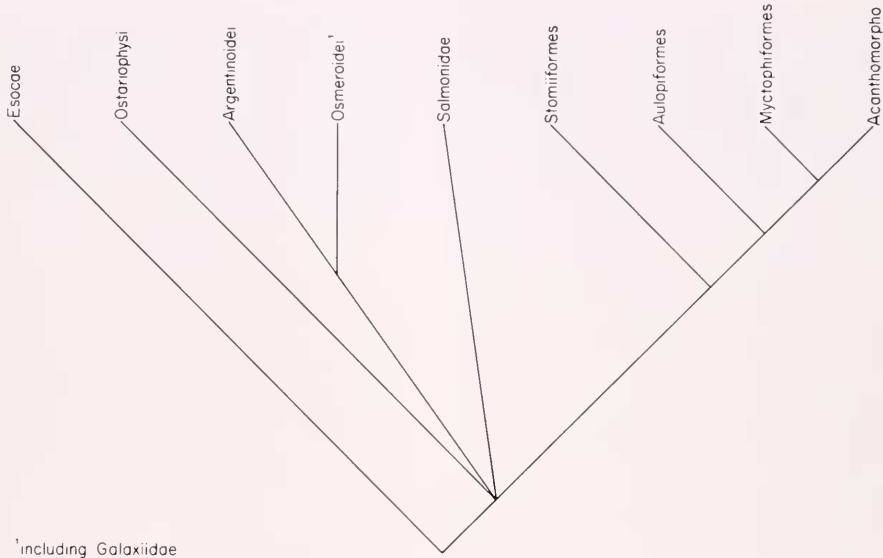


Figure 23. Summary cladogram of the hypotheses suggested from our survey of primitive euteleostean groups. Relationships of aulopiforms, myctophiforms, and acanthomorphs from Rosen, 1973.

This bone is present in most primitive teleosts, including esocoids, argentinoids, salmonids, and stomiiforms. A basisphenoid is not present in ostariophyans (Fink and Fink, 1981).

Third, osmeroids and galaxiids also lack an orbitosphenoid bone. An orbitosphenoid is present in most primitive teleosts, but is also lacking in the salmonid *Thymallus* (Norden, 1961), in some species of *Coregonus* (Norden, 1961), and in stomiiforms.

The presence of large, serially arranged mesopterygoid teeth in osmeroids and galaxiids, unique within the elopoccephalans, together with the absence of orbitosphenoid and basisphenoid bones, supports the placement of galaxiids within the osmeroid assemblage. Rosen listed all family level groups in the Osmeroidea as *incertae sedis*; we would add to that list the Galaxiidae, pending further work. The possibility of relationship of *Lepidogalaxias* to the osmeroids has been noted above, based on the presence of serially arranged teeth on the mesopter-

ygoid; the two authors who have examined this fish (Mees, 1961 and Rosen, 1974) disagree on whether those teeth are present.

Two features suggest that the salmonids may be more closely related to the neoteleosts than to the rest of the "protacanthopterygians." The first of these is the configuration of the posterior neurocranium and the articulation of the skull with the anterior vertebra. In salmonids, the exoccipital as well as the basioccipital articulates with the anterior vertebra. In *Brachymystax* and *Thymallus* (see Norden, 1961, Pl. 2 for *Thymallus*), exoccipital/basioccipital morphology is much as in *Diplophos*. In almost all non-neoteleostean and non-salmonid teleosts we examined, only the basioccipital articulates with the anterior vertebra. The only exception is *Hiodon*; as discussed above in the section on stomiiform relationships, the morphology of the articulation is quite different in *Hiodon* and the inclusion of the exoccipital in the joint seems clearly to be convergent.

The second feature is the presence of a cartilage structure between the ethmoid and the premaxillae. We have noted in the section on Relationships of the Stomiiformes that a rostral cartilage is a neoteleostean feature. This single, median cartilage body lies between the ethmoid and the premaxillae (see Fig. 4). In a number of primitive teleosts there is a pair of cartilage bodies or ossifications which articulate between the ethmoid, palatine, and, often, the maxilla of each side. Patterson and Rosen (1977) term a large, tightly articulated ossification in this position the ethmopalatine and note that smaller but possibly homologous elements are present in esocoids, cyprinoids (=Cypriniformes, *sensu* Fink and Fink, 1981), mormyroids and notopterids. Fink and Fink (1981) have also found them in *Chanos* and some characiforms. We have observed paired cartilage bodies in several salmonids also, but they lie in a unique configuration strongly suggestive of the rostral cartilage. The cartilages lie anterior rather than lateral to the ethmoid, near or along the midline, and are attached to the premaxillae. Among the fishes we examined, the largest of these bodies were found in *Prosopium*; in this fish they are paired blocks which meet at the midline.

It is our suggestion that basioccipital/exoccipital morphology, described above, and the presence of medial cartilage bodies between the ethmoid region and the premaxillae, both provide evidence for a realignment of the salmonid fishes as the sister group of the Neoteleostei. Evidence for relationship of the salmonids with argentinoids and osmeroids (including galaxiids) consists of the presence of enlarged teeth along the margin of the basihyal and platelike bone on some neural and hemal spines.

In summary of this section, we have surveyed the morphology of teleosts previously considered closely related to stomiiforms, primarily using Rosen's (1974)

analysis of relationships of the "protacanthopterygian" groups. A thorough morphological study will be needed to test Rosen's hypotheses in detail, but we have found some evidence in the course of the current study which may aid in setting the directions for future research. First, we are unable to conclude that the Protacanthopterygii is a monophyletic group. Esocoids seem to share no unique specializations with the other included taxa; we could list esocoids as *sedis mutabilis* at the euteleostean level or as the sister group of all other euteleosts, depending on placement of the ostariophysans. Second, we have expressed some reservation about inclusion of *Lepidogalaxias* with the esocoids. Third, we have doubts about a hypothesis of monophyly of the Argentinoidei plus Salmonoidei plus Osmeroidei (Infraorder Salmonae) and have discussed the three characters which may diagnose the group. Fourth, we agree with Greenwood and Rosen (1971) on the monophyly of the Argentinoidei, as diagnosed by them. Fifth, no features have yet been suggested to support the proposed hypothesis of relationship among the osmeroids, salmonids, and galaxiids. We agree with Rosen's placement of retropinnids (*Retropinna*, *Stokelia*, and *Prototroctes*), plecoglossids, salangids and osmeroids as unresolved sister taxa, but we would add to that group (Rosen's Osmeroidei) the Galaxiidae (Galaxiinae and Aplocheitoninae). And, finally, we have found some characters which can be interpreted as suggesting a sister group relationship between salmonids and neoteleosts.

The Ostariophysi, a major primitive euteleostean lineage, has not been dealt with in detail since the group historically has never been considered relevant to stomiiform relationships and we have found no evidence to suggest that it is. Lack of a toothplate over the fourth basibranchial is a character ostariophysans share with all non-esocoid euteleosts. In-

terrelationships of the major ostariophysan lineages have been recently analyzed by Fink and Fink (1981).

This much is clear from our survey of the "basal" euteleosts—much work remains to be done before we have a stable hypothesis of the relationships of these major phylogenetic lineages.

SUMMARY

1. Two of the species of *Diplophos*, *D. maderensis* and *D. taenia*, are described osteologically. Certain muscles and other parts of the soft anatomy are also described.

2. Monophyly of the Stomiiformes is documented by eight synapomorphic characters, including: 1) photophore morphology, 2) Type 3 tooth attachment mode, 3) a particular subdivision of the adductor mandibulae muscle, 4) rostromethmoid-premaxilla ligament extending from the ethmoid to the contralateral (and sometimes also the ipsilateral) premaxilla, 5) a single, broad, proximal termination of the second epibranchial which articulates with both the second and third pharyngobranchials, 6) posterior branchiostegal abruptly larger than those more anterior, 7) some branchiostegals articulating on the ventral hypohyals, and 8) rete mirabilia and associated blood vessels located at the posterior of the swimbladder.

3. Monophyly of the Neoteleostei is documented by four synapomorphic characters, including: 1) a retractor dorsalis muscle, 2) a rostral cartilage, 3) Type 4 tooth attachment mode, and 4) exoccipital and basioccipital bones both articulating with the vertebral column.

4. Monophyly of the Eurypterygii is discussed in the context of Rosen's (1973) analysis; the group is tentatively accepted as natural, primarily diagnosable by presence of a toothplate fused with the third epibranchial.

5. The primitive teleostean group Prot-

acanthopterygii, most recently defined (Rosen, 1974) (see Fig. 22) to include the Esocoidei, Argentinoidei, and Salmonoidei (including the Salmonoidea and Osmeroidea) may be an artificial assemblage. We find no evidence to consider esocoids closely related to the other members of the group. The Argentinoidi plus Salmonoidei may be monophyletic, based primarily on presence of enlarged teeth along the margin of the basihyal, but there is also evidence which suggests that the Salmonoidei is not monophyletic and that salmonids may be the sister group of the Neoteleostei. Galaxiids (including the Aplochitoninae) are considered to be osmeroids, rather than "salmonoids" as proposed by Rosen (1974). Our alternative hypothesis of relationships of the "basal" euteleosts is summarized in Figure 23.

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APPENDIX

Material examined, listed by family. Within a family, genera are listed alphabetically. For specimens which were cleared and stained, we include number of specimens examined, their standard lengths, and "CS." Specimens which were dissected are noted by "D"; skeletons are designated by SK. Specimens which were examined externally only are listed simply by museum number. Museum acronyms are DANA (Carlsberg Foundation Dana Collections), ISH (Institut für Seefischerei, Hamburg), MCZ (Museum of Comparative Zoology, Harvard University), SU (Stanford University, collection now housed at the California Academy of Sciences, San Francisco), and USNM (National Museum of Natural History, Washington, D.C.).

TAXON	MUSEUM NO.	NO.	SIZE (mm)	PROC.
Osteoglossidae				
<i>Scleropages</i> sp.	MCZ 54924	1	61.6	CS
Hiodontidae				
<i>Hiodon tergisus</i>	USNM 167970	2	70–72	CS
Elopidae				
<i>Elops saurus</i>	USNM 128290	2	67.0–111.2	CS
Megalopidae				
<i>Megalops cyprinoides</i>	USNM 199836	2	68.0–73.0	CS
Denticipitidae				
<i>Denticeps clupeioides</i>	USNM 195992	1	DAMAGED	CS
<i>Denticeps clupeioides</i>	MCZ 56428	1	32.6	CS
Chirocentridae				
<i>Chirocentrus dorab</i>	MCZ 41825	2	DAMAGED	CS
Clupeidae				
<i>Dorosoma smithi</i>	USNM 225024	1	56.2	CS
<i>Etrumeus sadinia</i>	USNM 188950	2	80–81	CS
Umbridae				
<i>Dallia pectoralis</i>	USNM 111643	1	112.8	CS
<i>Umbra limi</i>	USNM 193184	1	58.7	CS
Esocidae				
<i>Esox niger</i>	MCZ 56945	2	91.1–94.0	CS
Argentinidae				
<i>Argentina striata</i>	USNM 188224	2	112–125	CS
<i>Glossanodon struhsakeri</i>	USNM 36418	1	117.0	CS
Bathylagidae				
<i>Bathylagus ochotensis</i>	USNM 199826	1	DAMAGED	CS
Salmonidae				
<i>Brachymystax lenok</i>	USNM 105110	1	112	CS
<i>Coregonus stanleyi</i>	MCZ 52007	1	146	D,CS
<i>Coregonus</i> sp.	MCZ uncat.	1		SK
<i>Coregonus</i> sp.	MCZ uncat.	1		SK
<i>Cristivomer namaycush</i>	MCZ 52577	1	131	CS
<i>Hucho hucho</i>	MCZ 7003			
<i>Prosopium coulteri</i>	USNM 102375	2	84.8–88.2	CS
<i>Salmo gairdneri</i>	CAS(SU) 49265	4	68–72	CS
<i>Thymallus arcticus</i>	MCZ 32362			
Osmeridae				
<i>Hypomesus pretiosus</i>	MCZ 32720	1	156.0	CS
<i>Hypomesus pretiosus</i>	USNM 10472	4	92–116	CS
<i>Mallotus villosus</i>	USNM 130301	3	87.8–104.7	CS
<i>Mallotus villosus</i>	MCZ 39849			
<i>Osmerus mordax</i>	MCZ 56535	1	154.0	CS
<i>Osmerus mordax</i>	MCZ 57013	2	40.5–58.1	CS
<i>Spirinchus thaleichthus</i>	MCZ 104689	2	108.5–115.6	CS
Plecoglossidae				
<i>Plecoglossus altivelis</i>	MCZ 4014			
<i>Plecoglossus altivelis</i>	MCZ 29028			

APPENDIX. Continued.

Retropinnidae					
<i>Prototroctes muraena</i>	MCZ 6867				
<i>Retropinna retropinna</i>	USNM 201161	1	78.9		CS
Salangidae					
<i>Salanx microdon</i>	MCZ 25485				
Galaxiidae					
<i>Aplochiton zebra</i>	MCZ 46272				
<i>Brachygalaxias bullocki</i>	MCZ 46306	21	25-30		CS
<i>Galaxias maculatus</i>	MCZ 46301	20	45-65		CS
<i>Galaxias anomalus</i>	MCZ 46293	14	25-57		CS
<i>Galaxias delfini</i>	MCZ 46284	2	44-71		CS
		1			D
Gonostomatidae					
<i>Cyclothone pallida</i>	MCZ 56961	2			D
<i>Diplophos greyae</i>	USNM 135691	1	105.8		CS,part
<i>Diplophos maderensis</i>	MCZ 54303	1	110		CS
<i>Diplophos maderensis</i>	MCZ 56952	1			D
<i>Diplophos maderensis</i>	USNM 186282	1	111.5		CS
<i>Diplophos rebaini</i>	USNM 225012	1	252.0		CS,part
<i>Diplophos rebaini</i>	ISH 543-76	1			
<i>Diplophos rebaini</i>	ISH 73-76	1			
<i>Diplophos taenia</i>	MCZ 54302	1	184.3		CS
<i>Diplophos taenia</i>	MCZ 52536	1			D
<i>Diplophos taenia</i>	MCZ 52569	1			D
<i>Diplophos taenia</i>	MCZ 52548	3	34.0-62.0		CS
<i>Diplophos taenia</i>	MCZ 55469	1			D
<i>Diplophos taenia</i>	USNM 206614	1	171.0		CS
<i>Gonostoma elongatum</i>	MCZ 53133		233.0		CS
<i>Gonostoma elongatum</i>	MCZ 56964	1			D
<i>Margrethia obtusirostra</i>	MCZ 56967	1			D
<i>Triplophos hemingi</i>	USNM 199832	1	175		CS
Sternoptychidae					
<i>Argyropelecus lychnus</i>	MCZ 56948	1			D
<i>Argyropelecus offersi</i>	MCZ 56969	1			D
<i>Maurollicus muelleri</i>	MCZ 56949	1			D
<i>Polyipnus polli</i>	MCZ 56965	1			D
Photichthya*					
<i>Aristostomias grimaldii</i>	MCZ 57014	1	140.0		CS
<i>Astronesthes</i> sp.	MCZ 56951	1			D
<i>Astronesthes gemmifer</i>	MCZ 42864	1			D
<i>Astronesthes lucifer</i>	USNM 225046	1	141.8		CS
<i>Chauliodus schmidtii</i>	USNM 225045	4	51.2-165.0		CS
<i>Echiotoma</i> sp.	USNM 199839	2	264.7-275.7		CS
<i>Heterophotus ophistoma</i>	USNM 225025	2	133.2		CS
<i>Ichthyococcus irregularis</i>	USNM 201385	1	39.5		CS
<i>Idiacanthus fasciola</i>	DANA 3784-VIII	1	323.3		CS
<i>Idiacanthus fasciola</i>	MCZ 57012	1	470.0		CS
<i>Macrostomias longibarbus</i>	USNM 225035	1	205.5		CS
<i>Malacosteus niger</i>	MCZ 53286		124.1		CS
<i>Melanostomias</i> cf. <i>biseriatus</i>	USNM 199847	1	193.5		CS
<i>Melanostomias</i> sp.	MCZ 56955	1			D
<i>Neonesthes capensis</i>	USNM 199823	1	114.1		CS
<i>Photichthys argenteus</i>	MCZ 56953	1			D
<i>Photichthys argenteus</i>	MCZ 56950	1			D
<i>Photichthys argenteus</i>	USNM 203407		93.1		CS
<i>Photonectes margarita</i>	MCZ 57010	1	159.0		CS

* Infraorder, not divided into families.

APPENDIX. Continued.

<i>Photostomias guernei</i>	USNM 225027	1	127.2	CS
<i>Pollichthys mauli</i>	USNM 201278	2	32.5–35.0	CS
<i>Pollichthys mauli</i>	MCZ 56954	1		D
<i>Polymetme corytheola</i>	MCZ 56968	1		D
<i>Polymetme corytheola</i>	MCZ 40918	1		D
<i>Polymetme corytheola</i>	USNM 199507	1	174.0	CS
<i>Polymetme corytheola</i>	USNM 225166	1		D
<i>Rhadinesthes decimus</i>	USNM 225044	1	325.0	CS
<i>Stomias boa</i>	MCZ 53384	1	225	CS
<i>Tactostoma macropus</i>	MCZ 57011	1	168.0	CS
<i>Tactostoma macropus</i>	USNM 187654	1	124.4	CS
<i>Trigonolampa miriceps</i>	USNM 206683	1	166.9	CS
<i>Vinciguerrria lucetia</i>	USNM 201315	12	17.0–47.6	CS
<i>Woodsia nonsuchae</i>	MCZ 49083	1		D
Aulopidae				
<i>Aulopus filamentosus</i>	USNM 225043	2	143–173	CS,D
<i>Aulopus nanai</i>	MCZ 40516	1		D
Bathysauridae				
<i>Bathysauris mollis</i>	MCZ 40518	1		D
Chlorophthalmidae				
<i>Chlorophthalmus agassizii</i>	MCZ 40539	1		D
<i>Chlorophthalmus agassizii</i>	USNM 159377	1	121	CS
Synodontidae				
<i>Synodus intermedius</i>	MCZ 46617	1	123	CS
		1		D
Paralepididae				
<i>Paralepis elongata</i>	MCZ 43129	1	129	CS
Neoscopelidae				
<i>Neoscopelus macrolepidotus</i>	MCZ 35596	1		D
<i>Neoscopelus macrolepidotus</i>	USNM 188056	2	116–117	CS,D
Myctophidae				
<i>Lampanyctus iselinoides</i>	MCZ 52900	1		D
<i>Lampanyctus tenuiformis</i>	MCZ 56963	1		D
<i>Lepidophanes guentheri</i>	MCZ 56960	1		D
<i>Myctophum affine</i>	MCZ 56947	2	62.6–70.0	CS
<i>Myctophum asperum</i>	MCZ 56966	1		D
<i>Notoscopelus kroyeri</i>	MCZ 55532	1		D
<i>Taaningichthys bathyphilus</i>	MCZ 53796	1		D
<i>Talismania homoptera</i>	MCZ 51959	1		D
<i>Triphoturus mexicanus</i>	MCZ 56962	1		D
Percopsidae				
<i>Percopsis omiscomaycus</i>	MCZ 41221	1	56	CS
Apogonidae				
<i>Synagrops microcephalus</i>	MCZ 56946	1	54.3	CS
Percidae				
<i>Perca flavescens</i>	MCZ 48920	1	68.4	CS
Coryphaenidae				
<i>Coryphaena hippurus</i>	MCZ 56944	1	69.5	CS